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MORPHOLOGICAL AND PALEOBOTANICAL
STUDIES OF THE NYSSACEAE, I
A SURVEY OF THE MODERN SPECIES AND THEIR FRUITS

RICHARD H. EYDE

THE LIVING SPECIES OF the genus *Nyssa* L. are native in eastern North America and in eastern Asia. This widely disjunct distribution is a familiar pattern to students of plant geography, for many other woody genera have a similar range. It is generally accepted that such genera are the remnants of an ancient mesophytic forest that extended throughout most of the northern hemisphere during Tertiary times (Li, 1952). In the case of *Nyssa*, this wide former distribution cannot be doubted, for fossil *Nyssa* remains are found in various Tertiary strata across Europe, Asia, and North America. Since these remains include fruits, pollen, and wood, as well as leaves, it may be said fairly that *Nyssa* has one of the best fossil records of any modern genus of trees.

The fossil fruits of *Nyssa* are particularly interesting because they are frequently found in an excellent state of preservation and because they exhibit a diversity of form that makes it possible to compare them with fruits of the most closely related living species of *Nyssa*; yet the fossils are often sufficiently different from their modern counterparts that one can study some of the evolutionary changes which have taken place within the genus. One of the world's best sources of fossil *Nyssa* is the early Tertiary brown coal of Brandon, Vermont. The largest, most distinctive fruits to be found in this richly fossiliferous deposit are those of *Nyssa*; they are present in such abundance that they were collected as "beechnuts" by 19th century miners. Moreover, the Brandon nyssas are so variable in size and shape that one investigator assigned them to 10 genera and to more than 50 fossil "species."

The investigations to be described here began with the most recent excavation of the Brandon deposit by Barghoorn and associates during 1947 and 1948, at which time many hundreds of *Nyssa* fruits were collected, cleaned, and separated into tentative morphological categories. Preliminary comments on these fruits may be found in the descriptions of the Brandon lignite and its flora by Barghoorn (1950) and by Barghoorn and Spackman (1949). Microtome sections were prepared from many of

these specimens, and fruits of modern *Nyssa* species were collected for comparative purposes, as it was intended that *Nyssa* should form an important part of a general morphological and systematic study of the Brandon fruits and seeds. This collection, together with photographs, bibliographical materials, and observational notes, was subsequently turned over to the author of this paper, who has continued the study of *Nyssa* as a graduate research program under the guidance of Professor Barghoorn.

As the investigation progressed it became apparent that the evolutionary significance of the Brandon nyssas could not be evaluated without first studying the external and internal structure of related modern fruits. It became equally apparent that a treatment of fossil *Nyssa* should include a critical survey of as many *Nyssa* remains as possible, and not just those from Brandon. No such survey has been attempted since the appearance of Kirchheimer's admirable monograph more than 20 years ago (1938), although the *Nyssa* record has been greatly increased since then, especially as a result of palynological research. Therefore the present work has been broadened to include both morphological and paleobotanical research on *Nyssa* and closely related genera, with special emphasis on the morphology of the fruits. It should be added that *Nyssa* and allied genera include some of the most primitive living members of the Umbellales. It is to be hoped that the research reported here will not only aid in understanding the relationships between the taxa studied, but will also shed some light on the origin of this order of angiosperms.

The present paper will deal with the living species of *Nyssa* and their fruits; the fossils will be treated in a later report.

FAMILY CHARACTERISTICS

The genus *Nyssa* and the related monotypic genera *Camptotheca* Decne. and *Davidia* Baill. may be treated systematically as a single family Nyssaceae or as two subfamilies, Nyssoidae and Davidioideae, within the Cornaceae *sensu lato*. In any case, the affinity with Cornaceae and other families of the Umbellales is well supported by morphological and anatomical evidence and has been recognized for many years.

The criteria that have been used for separation of Nyssaceae from the Cornaceae are not altogether satisfactory. Hutchinson (1959, p. 94) cites the presence of imbricate petals as a key character for recognizing Nyssaceae; however petals of the cornaceous genera *Griselinia* Forst. f. and *Melanophylla* Baker also are said to be imbricate in the bud (Harms, 1898; Horne, 1914), and in the case of the nyssaceous *Camptotheca* the overlapping of petal edges is often so slight as to be scarcely perceptible. Wangerin distinguished Nyssaceae from Cornaceae on the basis of "Diplostemonie der Blüten, doppeltes Integument des Ovulums und Ausbildung des Pollens" (1910, p. 7). The last two of these distinctions may now be discounted; the similarity of pollen grains in the two families has been pointed out by Erdtman (1952, p. 290), and the absence of a second integument has been noted by Horne (1909, 1914) and by Titman (1949).

Wangerin's use of diplostemony as a distinguishing feature of Nyssaceae retains some validity; it is evident when flowers of all species are examined that there is a tendency for stamens to occur in two series in staminate flowers; however this tendency is somewhat obscured in some species by a marked variability in the numbers of floral appendages. In any case, the number of stamens is greater in flowers of Nyssaceae than in Cornaceae *sensu stricto*, whether or not two series are detectable.

The flowers of Nyssaceae have features in common with those of other members of the Umbellales, e.g., an inferior ovary and a solitary seed in each locule, but the nyssaceous genera are unlike most others in the order in that there are two kinds of flowers, staminate and hermaphrodite.¹ In *Nyssa* and *Camptotheca* the staminate and hermaphrodite flowers are borne on separate inflorescences, and in *Nyssa* the two different kinds of inflorescence are borne on separate plants. The *Davidia* inflorescence is unique in that a single hermaphrodite flower arises from a densely capitate inflorescence in which all other flowers are staminate.

This report will include morphological observations and distributional data not only for all species of Nyssaceae but, to some extent, for the cornaceous genus *Mastixia* Blume as well. *Mastixia* is customarily treated as the only genus of the subfamily Mastixioideae of the Cornaceae, and inclusion of it in the present work is not meant to imply any disagreement with that treatment; however, there is no doubt that the mastixioids, as members of the Cornaceae, have some degree of relationship with Nyssaceae. Moreover, there are two compelling reasons for giving some attention to *Mastixia* in seeking clues to evolutionary trends in the Nyssaceae. First, with regard to its secondary xylem, *Mastixia* is the most primitive genus of Cornaceae and, along with *Davidia*, of the order Umbellales (Adams, 1949; Li and Chao, 1954; Rodriguez, 1957, p. 274); therefore it is not unreasonable to look to this genus for other primitive characters. Secondly, *Mastixia*, like *Nyssa*, has an excellent fossil record, against which evolutionary concepts eventually may be tested.

FIELD AND HERBARIUM STUDIES

The author has made continual use of the Nyssaceae preserved in the Gray Herbarium and the herbaria of the Arnold Arboretum and the New England Botanical Club throughout the course of this investigation. *Nyssa* collections were also examined in the herbaria of the following institutions: the New York Botanical Garden; the Royal Botanic Gardens, Kew; the Indian Botanic Garden, Calcutta; and the U.S. National Museum. In addition, an important collection of *Nyssa javanica* specimens was sent on loan

¹The term "hermaphrodite" is used here to emphasize that both gynoeceum and androeceum are present; however the fertility of the androeceum in these flowers has never been critically investigated. Judging from the material examined by the author, pollen is usually produced by hermaphrodite flowers of some Nyssaceae (e.g., *Camptotheca acuminata*), but in other species (*Nyssa aquatica*, *N. ogeche*) pollen is produced infrequently or not at all. In hermaphrodite flowers of *N. sylvatica* some anthers contain apparently normal pollen, and others are abortive.

from the Rijksherbarium, Leiden. The distribution maps presented in this paper are based on information obtained from these collections. It will be understood that the localities could not be plotted so precisely for Asiatic Nyssaceae as for the American species, since specimens collected in remote parts of Asia are often accompanied only by the collector's number, or by place-names known only locally. In the case of Chinese collections this difficulty was overcome by enlisting the aid of Dr. Shiu-ying Hu, who was able to establish approximate localities through her familiarity with the geography of China and with the travels of botanists who have collected there. For regions outside China, the *Times Atlas* and *Atlas van Tropisch Nederland* were consulted. Although a few of the localities still remain unknown to the author except in a general way, e.g., "North Burma" and "Tonkin," the ranges for Asiatic Nyssaceae as shown here are far more accurate than any previously available in the literature.

Fruits of all the American species of *Nyssa* were collected from living trees during a field trip conducted especially for that purpose in August, 1959. The trip included visits to the lower Apalachicola River in Florida, to the Okefenokee Swamp in Georgia, to the Dismal Swamp in Virginia, and to several other localities where *Nyssa* grows in abundance. Flowers and developing fruits of *N. sylvatica* and flowers of *Davidia involucrata* were collected in preservative at the Arnold Arboretum, and preserved flowers of some of the other species were graciously supplied by Drs. W. P. Adams, Clyde Connell, R. K. Godfrey, and Carroll E. Wood, Jr.

Research on *Nyssa* was interrupted during part of 1960–61 when the author accepted a foreign study fellowship in India; however the trip provided an unexpected opportunity to see *N. javanica* in one of its native habitats, the eastern Himalaya. Accordingly, in May of 1961, when the trees had come into flower, a visit was made to the Darjeeling Hills and specimens obtained were preserved in fixative. Mr. G. C. Sen, Curator of the Lloyd Botanic Garden, Darjeeling, gave assistance in planning this collecting trip; acknowledgment is gratefully extended to him. Acknowledgment is also due to the authorities of the various herbaria for the loan of specimens and facilities, and to the Botany Department, University of South Carolina, for several courtesies.

SURVEY OF THE SPECIES

It seems advisable to discuss specific similarities and differences among the Nyssaceae before entering into a detailed descriptive treatment of their fruits. Information regarding the present distribution and habitat of each species is included as a possible aid in the interpretation of the fossil record. It will be seen that four of the species of *Nyssa* — *N. sylvatica*, *N. aquatica*, *N. ogeche*, and *N. javanica* — differ markedly from each other in many ways, including the appearance of their fruits; on the other hand, *N. sylvatica*, *N. sinensis*, and the putative species *N. biflora* and *N. ursina* are very similar, and it is not possible to assign an unattached fruit to any one of these species with certainty. Since the emphasis of

this paper is on fruits, the latter group will be discussed under one heading, "the *Nyssa sylvatica* complex."

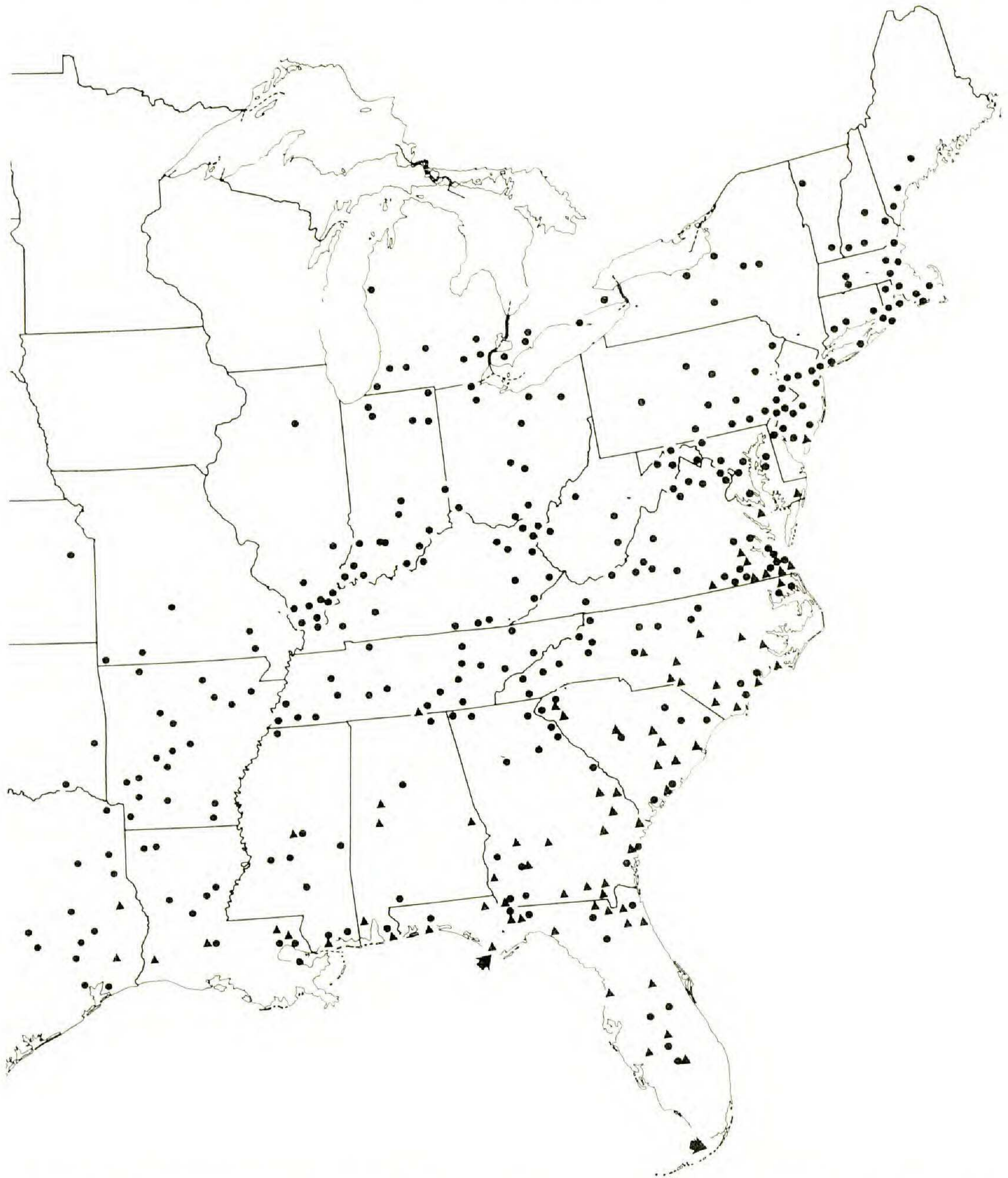
The *Nyssa sylvatica* Complex

NYSSA SYLVATICA Marshall. This common tree of the eastern United States is usually recognizable by its branching habit; most of the very crooked branches leave the trunk almost at right angles, sometimes giving the tree a pyramidal aspect when growing in the open. It frequently attains a height of more than 20 meters; the largest known living tree of this species is 85 feet² (Dixon, 1961), and even taller trees have been reported in the past (Anon., 1942). On the other hand, this species and other members of the genus can produce vigorous shoots from the roots and lower stem, resulting in shrubby growth and the formation of thickets. The leaves of *N. sylvatica*, like those of other species of *Nyssa*, are alternate, simple, pinnately-veined, estipulate, and commonly crowded at the ends of branches; they turn red in the fall, and for this reason *N. sylvatica* is sometimes planted as an ornamental tree. Leaf margins are almost always entire, but some leaves with a few coarse teeth may occur on any individual, and are fairly common on seedlings and sprouts. Papillae are often visible on the leaf surfaces, probably caused by the sclereids that are present within the mesophyll (Metcalf and Chalk, 1950, p. 750). For further details regarding the vegetative parts of *N. sylvatica* and of other American nyssas, the reader is referred to the works of Rickett (1945) and Sargent (1893, 1922).

Flowers of *Nyssa* are first visible in the Arnold Arboretum during the latter part of May, when the young leaves are not yet fully developed. Certain trees bear staminate flowers in short racemes; others bear hermaphrodite flowers in clusters of two, three, or four on slender peduncles.

The range of *Nyssa sylvatica* includes all of the eastern United States from Kennebec County, Maine, south to Lake Okeechobee in Florida, west to the Brazos River in Texas, and north to the Great Lakes, where the species also occurs in the southern part of Canada (MAP 1). It is a familiar tree in the mixed mesophytic forest of the Appalachian Plateaus, the oldest and most complex type of deciduous forest in North America. In the Cumberland Mountains of eastern Kentucky, believed by Braun (1950) to be the region where the American mixed mesophytic forest is best developed, *N. sylvatica* is one of about 35 species comprising the canopy. *Nyssa* is scattered here and there throughout the region, a few individuals occurring in most stands regardless of exposure or altitude, yet contributing little to the total vegetative cover (Braun, p. 52-53). The species is typically one of "high presence-low cover" in other forested areas as well (see, for instance, Braun's tables, p. 139, 167, 246, etc.; also McIntosh, 1959); however, local concentrations of these trees may occasionally be found in unusually wet places (Baldwin, 1961).

² English units of measurement will be used in this paper when necessary to preserve the reports of other authors, data from herbarium sheets, etc., in their original form.



MAP 1. Distribution of the *Nyssa sylvatica* complex in U.S. and Canada. County records for *N. sylvatica* are represented by black circles, for *N. biflora* by triangles. Arrows show localities from which "*N. ursina*" has been collected.

The juicy ripe fruits of *Nyssa sylvatica* are very attractive to birds, which are probably the most important agents of dispersal. During the present investigations gnawed endocarps have been collected, suggesting that rodents may also participate in dispersing the species. Pollination is presumably effected for the most part by the hosts of bees and other insects that visit the flowers, but Wodehouse reports the collection of air-borne pollen about 500 feet from a tree (1935, p. 446).

In 1944 Miranda reported the first collections of *Nyssa sylvatica* in Mexico. In subsequent papers, Sharp and Hernandez X. (1945) and Miranda and Sharp (1950) described the localities in which *Nyssa* has

been found. The sites are located in highlands of Hidalgo, Puebla, and Chiapas (MAP 2), areas of considerable phytogeographical interest because they support a vegetation resembling that of the eastern United States yet containing elements with other geographical affinities. *Nyssa* has been collected here at altitudes up to 6200 feet, but it is most plentiful between 3300 and 5000 feet, where it is associated with *Liquidambar* in forests in which mixed species of *Quercus*, *Platanus lindeniana*, *Pinus strobus*, or *Liquidambar* may be dominant, depending upon the locality. In most of the Mexican sites, *N. sylvatica* is a tree in the upper layer of the forest, but in the vicinity of Huachinango, Puebla, it has been found only in the form of sprouts and small trees. Sharp and Hernandez X. suggest that this may be due either to periodic burning or to the activities of woodcutters.

In handling a large number of herbarium specimens of *Nyssa sylvatica* one becomes impressed with the great range of variability in the size and shape of the leaves. This amount of variation led Fernald (1935) to distinguish four varieties (var. *biflora* (Walt.) Sarg., var. *dilatata* Fern., var. *caroliniana* (Poir.) Fern., and var. *typica* which must now be called var. *sylvatica*). The author has attempted to recognize these varieties in the course of his herbarium studies and field work but has found it impractical because of the many intergradations and lack of clear geographical segregation to distinguish more than two — var. *sylvatica* and var. *biflora*.

In 1893 Sargent reduced *Nyssa biflora* Walt. to varietal rank under *N. sylvatica*, but in 1905 (Man. 709) he treated it as a distinct species. In



MAP. 2. Distribution of *Nyssa sylvatica* in Mexico. Data from Sharp and Hernandez X. (1945). (Copyright, Goode Base Maps.)

many modern floras this practice is also followed, but Rehder, in his *Bibliography of Cultivated Trees and Shrubs* (p. 485), maintains *N. sylvatica* var. *biflora*. In the interest of brevity, the name *N. biflora* will be used throughout the present work, although the taxon is not considered equivalent in rank to *N. sylvatica* and its real status must remain somewhat uncertain until the results of more observations are evaluated.

NYSSA BIFLORA Walter. There are large numbers of trees of *Nyssa* growing in upland swamps and wet bottomlands of the Coastal Plain of the southeastern United States (MAP 1) that are clearly allied with *N. sylvatica* yet sufficiently different in some respects to be treated as a separate taxon, *N. biflora*. These trees are commonly found in great abundance in saturated soil and in standing water, where they often develop enlarged bases. Their leaves are smaller and more leathery than those of *N. sylvatica*,³ and are of a different shape.

The leaf of *N. biflora* is commonly narrower in outline and more gradually tapered at the base, and sometimes more rounded at the apex as well. The fruiting peduncle is usually not so long as in *N. sylvatica*. *N. biflora* with fruits on long peduncles is not uncommon, and *N. sylvatica* with fruits on relatively short peduncles may be found. A difference in the number of hermaphrodite flowers borne on each peduncle is notable. In *N. sylvatica* two, three, or four flowers occur — a single flower is quite rare. In *N. biflora* although the number of flowers is usually two, as the name implies, solitary flowers are not unusual, and clusters of three may be found, but not clusters of four.

Trees of *Nyssa biflora* flourish in water of sufficient depth to discourage the growth of most other woody plants. *Taxodium* and sometimes *Nyssa aquatica* are associated with it within the swamp forest, but there are no other dominant trees, and the density of each of these species is extremely great. Pure stands of *N. biflora* may also occur, according to Hall and Penfound (1939) who described a virgin swamp forest of southeastern Louisiana in which only this species was important. The individual trees averaged 83 feet in height and were estimated to be 200 years old. In the shallower water at the edges of such swamps species of *Acer*, *Planera*, *Fraxinus*, *Salix*, *Quercus*, *Pinus*, *Magnolia*, *Ilex*, *Cyrilla*, *Zenobia*, and other genera may be found in association with *N. biflora*, depending upon local conditions (Wells, 1942; Penfound, 1952).

The different habitat occupied by *Nyssa biflora*, combined with the somewhat different range of variability in leaf and fruiting characters, mark it as something apart from *N. sylvatica*; however it is not always possible to assign individual plants to either taxon. There are numerous trees of *Nyssa* growing in more or less wet places of the Coastal Plain and adjacent regions bearing leaves intermediate in size and shape between the broad obovate form agreeing with *N. sylvatica* and the narrow oblanceolate form agreeing with *N. biflora*. Such trees may also bear fruits in clus-

³ Philpott (1956) has described the anatomical differences that accompany this difference in leaf shape and texture. For dimensions of *Nyssa* leaves, see Rickett (1945).

ters of two and three on stalks of varying length. This situation has led some workers to treat *N. biflora* in a rank below that of species. Rickett (1945) has preferred to treat both *N. biflora* and *N. sylvatica* as species, suggesting that hybridization occurs between the two. A satisfactory solution to this problem would require an intensive investigation of genetic⁴ and environmental⁵ factors. It is quite possible that an investigation of this kind would show that we are dealing with a stage in speciation, in which part of a very variable population has become adapted to a separate ecological niche, the swamp, but has not yet become entirely isolated from the older gene pool by the formation of reproductive barriers.

The problem of specific limits and distinctions within the *Nyssa sylvatica* complex is made even more intricate by the occurrence in western Florida of shrubby forms that are extreme in the small size, narrow elliptic shape, and leathery texture of their leaves. The fruits of these plants are frequently smaller and much more globular and fleshy than those usually encountered in *N. biflora*, and fruiting peduncles are the shortest in the genus. Hermaphrodite flowers are mostly in pairs, and staminate flowers are few on short peduncles. These shrubby nyssas were first discovered in swamps of the Apalachicola River delta by Small (1927), who described them as a new species, *N. ursina*. No additional localities for *N. ursina* were reported until quite recently, when Monachino and Leonard (1959, p. 184) found a specimen among some forty-year-old collections from the Florida Keys. Mr. Monachino kindly sent this material to the author for inspection. It is a fruiting specimen with fleshy fruits on short peduncles and small leathery leaves like those encountered on the Apalachicola delta.

A number of collections were made in the *Nyssa ursina* region as a part of the present investigation. The shrubby nyssas are very plentiful in standing water near the towns of Port St. Joe and Apalachicola, and they do, indeed, have a very different appearance from the tall trees of *N. biflora* found in virgin swamp forests. The most striking plants of all were seen growing in a bog with *Sarracenia* about two miles east of Overstreet, in Gulf County. These plants were very much branched, as if they had been pruned, and, although only about three feet tall, were in full fruit. In this locality the nyssas were clearly growing as separate plants; in many other localities the *Nyssa* growth was taller, 10 or 12 feet, and occurred in dense

⁴ *Nyssa* has never been a subject for genetic research, nor have the chromosomes been counted for any species save *N. sylvatica*. Dermen (1932) obtained a count of $2n = 44$ from root tips of this species at the Arnold Arboretum. As a matter of curiosity the author attempted to count the chromosomes in developing anthers of *N. biflora* supplied by R. K. Godfrey (RKG 58248). From the meiotic figures obtained, the chromosome number cannot be reported with any greater accuracy than $n = 22 \pm 1$.

⁵ One might well wonder whether the morphological differences that distinguish *Nyssa biflora* from *N. sylvatica* could be brought about by the swamp environment rather than by genetic factors. The author was able to locate a fruiting *N. biflora* growing under cultivation on dry ground in the arboretum of Brookgreen Gardens in South Carolina. Although this tree reportedly had been grown from seed in the garden, it showed all of the *N. biflora* characteristics. One must infer that these characters are inherent.

thickets not easily separable as individuals. From the town of Apalachicola northward through Franklin County to Sumatra, Florida, *Nyssas* with leaves intermediate between the extreme *N. ursina* form and the usual *N. biflora* form are in evidence; north of this transition zone there are full-sized plants of *N. biflora* and none referable to *N. ursina*.

Not all botanists who have observed the plants in the field are in agreement with Small's concept of *Nyssa ursina* as a distinct species. Professor R. K. Godfrey, of Florida State University, and Dr. W. P. Adams, now of DePauw University, have expressed the opinion in conversations with the author that the dwarfed, branching habit and the peculiarities of leaf form and peduncle length exhibited by *Nyssa* in the Apalachicola delta region are the result of periodic fires. The pruned appearance of the plants found growing near Overstreet does suggest that some factor, perhaps fire, has disrupted the normal apical growth of the branches. Moreover, the existence of intergradations between the extreme *N. ursina* characters and the usual *N. biflora* characters makes somewhat doubtful the concept of two separate species. It is relevant to add here that the globular drupes supposedly characteristic of *N. ursina* may occasionally be found elsewhere. Mr. Frank C. MacKeever collected such specimens from a tree on the island of Martha's Vineyard in Massachusetts and brought them to the attention of the author. The fruits on MacKeever's *MV 306* were quite plump and fleshy when collected, and they contain short, ovoid stones like those found in many fruits from the Apalachicola River delta; however, the fruiting peduncles and leaves of the Martha's Vineyard tree are those of *N. sylvatica*. Possibly globular fruits occur on *N. sylvatica* in other localities; the character is not readily detectable on dried herbarium specimens, which would account for the fact that such fruits have not previously been reported. Certainly a careful study of variation in *N. sylvatica* and *N. biflora* under different ecological conditions is needed before it will be possible to clarify the status of *N. ursina* satisfactorily.

NYSSA SINENSIS Oliver. The Chinese *Nyssa* is so similar in general vegetative and floral characteristics to *N. sylvatica* that its close relationship to the American species cannot be doubted. Notwithstanding, there are a number of morphological differences that clearly separate the two as distinct species. The Chinese species includes individuals with much larger leaves, often with more arcuate secondary nerves, than those usually produced by *N. sylvatica*. Young leaves, shoots, peduncles, and pedicels are more pubescent in the Chinese species, a condition which may persist into maturity. A dense pubescence is commonly noticeable on stalks of staminate inflorescences; less frequently so on fruiting peduncles and on petioles and midribs of leaves. Perhaps the most striking difference between *N. sinensis* and its American counterpart is in the occurrence of pedicels on the peduncles of hermaphrodite inflorescences; such structures are present only occasionally on American members of the *N. sylvatica* complex, but they are universal in the Chinese species. Where this character is most pronounced the pedicels are paired on the peduncle, suggesting that the

inflorescence has originated from a dichotomous branching system. The young pedicel is subtended in most cases by a bract which is deciduous early in the development of the fruit, leaving a scar. Hermaphrodite flowers are mostly four to a cluster, and peduncles bearing five are found.⁶ A further difference, of special interest in connection with the present work, is the common occurrence of two styles and a bilocular ovary in *N. sinensis*; the condition occurs only with great rarity in *N. sylvatica*.

Nyssa sinensis is widely distributed in hilly regions of the Yangtze Valley and in provinces of southern China. Specimens in the herbarium of the Arnold Arboretum and the Gray Herbarium have been collected from southern Kiangsu, southern Anhwei, northern Kiangsi, and eastern Szechuan; also from Kweichow, Hunan, Chekiang, Kwangsi, Kwangtung, Yunnan (MAP 3). According to Wang (1961, p. 123, 143), the species also



MAP 3. China, showing distribution of *Nyssa sinensis*.

occurs in western Szechuan and in southern Fukien, and Merrill (1938, p. 58) reported a specimen collected in the northern part of Tonkin (Vietnam). The westernmost collections so far have been made in the Shweli Valley of western Yunnan and in upper Burma. The Chinese species, like the nyssas of North America, may occur as tall trees (up to 30 m.) in the forest canopy or as shrubby growth along the banks of streams (Wilson, 1914; Hu, 1927).

Throughout much of its range, *Nyssa sinensis* is a member of the crown layer of the Chinese mixed mesophytic forest, a forest formation described

⁶ Clusters containing five flowers are not plentiful in *Nyssa sinensis*, but they are certainly not so rare as in American members of the complex. In the course of inspecting a far greater number of American nyssas in the herbarium and in the field, only one five-flowered cluster was encountered. Wangerin's statement that the pistillate flowers of *N. sylvatica* occur in clusters of two to eight (1910, p. 9, 11), repeated by Rickett (1945), is in error.

in detail in a recent monograph by Wang (1961). The formation resembles the mixed mesophytic forest of eastern North America in that it contains a large number of species of deciduous broad-leaved trees belonging to distantly related families; further resemblances are the homogeneity of the forest over broad geographic areas and the lack of dominance of any one species or group of species; however there is a signal difference in the floristic richness of the two regions. As Wang has pointed out (p. 236–237), the American mixed mesophytic forest, interpreted as broadly as possible, contains no more than 30 genera of dominant trees; whereas its Asiatic counterpart contains more than 60, including all but three of the 30 American genera. This richest of all deciduous forests extends for 2000 kilometers along the lower and upper Yangtze Valley and its watersheds. In the lower Yangtze Valley, a region of intense cultivation, remnants of the natural forest are found only in certain protected areas. (This explains the clustering of collection localities at some places on MAP 3.) There the mixed mesophytic formation covers the mountain slopes from altitudes of 500 to 1500 meters. The upper Yangtze region is one of higher elevations, in which the zone of deciduous forest is usually restricted to levels above 1500 meters, where it lies below a higher coniferous forest; at lower levels in this region, the constituents of the deciduous forest are mixed with evergreen broad-leaved trees (Wang, p. 120). It was within the upper Yangtze mixed mesophytic forest that living *Metasequoia* was discovered, and *N. sinensis* was one of the many deciduous broad-leaved trees found in association with this “living fossil” (Chu and Cooper, 1950). The Tsinling mountain range marks the northern limit of the mixed mesophytic forest and the beginning of a forest in which deciduous oaks predominate. To the south there is no boundary of any kind; deciduous trees become more and more intermixed with evergreen broad-leaved trees at increasing distances from the Yangtze Valley, until the evergreen trees predominate. It may be added that the Asiatic mixed mesophytic forest is also found in parts of Korea and Japan; however, *N. sinensis* has never been reported from either of these countries.

Collections of *Nyssa sinensis* have been obtained from several localities in the predominantly evergreen forest that lies to the south of the Chinese mixed mesophytic forest. This is a subtropical forest, dominated by evergreen species of *Castanopsis*, *Quercus*, and *Pasania*, along with *Schima* and lauraceous trees. The average temperature is not below five degrees Centigrade for any month, and no month is without rain. Total annual rainfall is 1300–1900 mm., somewhat higher than in the mixed mesophytic forest. Elevations are higher and conditions slightly more temperate in the areas where *Nyssa* and other deciduous trees are found as minor constituents (Wang, p. 142–146).

It is of considerable interest to compare the climatic conditions to which the Chinese nyssas and their New World counterparts are subjected. There are, as one would expect, numerous resemblances between the climate of the mixed mesophytic forest region of Asia and the climate of the equivalent North American forest region, but nowhere is the Chinese

species exposed to the rigorous winters endured by *Nyssa sylvatica* in the northeastern United States. Furthermore, the growing season is much shorter in the heart of the American mixed mesophytic forest than in similar forest areas of China. The growing season in the Cumberland Mountains of Kentucky is about 180 days (U.S. Dep. Agr. Yearbook, 1941); whereas there are 230–280 frost-free days in the Chinese mixed mesophytic forest (Wang, p. 96). This fact accounts, at least in part, for the greater richness of the Chinese forest. Climatic conditions at the southern part of the range of *N. sinensis* may be compared with those prevailing in parts of Florida and in the highlands of eastern Mexico, the two southernmost regions in the range of *N. sylvatica*.

Perhaps at some future date it will be possible to test the success of the Chinese *Nyssa* in our American climate, but at present there seem to be no trees of this species in the United States. It has, however, been introduced into England at least twice. There are references in the literature to a single plant grown in Veitch's nursery at Coombe Wood from seed sent in 1902 by E. H. Wilson (Bean, 1950). Evidently this plant is no longer in existence; however there is a small *N. sinensis* now growing behind the arboretum office at the Royal Botanic Gardens, Kew, introduced as seed sent from Nanking in 1935. This plant, set outdoors in 1960, seemed to have endured its first winter fairly well at the time the author inspected the plant in early June, 1961. It bore a few staminate flowers, but was only about eight feet high and the expanded leaves were not as big as those usually seen on herbarium specimens of *N. sinensis*. The leaves of this species, like those of *N. sylvatica*, turn red in the fall.

Other Species of *Nyssa*

There are three other species of *Nyssa* — *N. javanica*, *N. aquatica*, and *N. ogeche* — in which close interspecific affinity is not evident.

NYSSA JAVANICA (Blume) Wangerin. This is the only species of *Nyssa* in which both hermaphrodite flowers and staminate flowers are borne in capitate clusters. Staminate flowers are numerous, and each is on a pubescent pedicel subtended at its base by three small bracts.⁷ Hermaphrodite flowers are sessile and fewer in each head, but similarly associated with basal bracts. Branched inflorescences, with heads on each of two or three branches, occur occasionally in *N. javanica* but in no other species of *Nyssa*. The leaves are more leathery than those of *N. sinensis*, and they often develop a prominent "drip-tip." A distinguishing feature of *N. javanica* to be given special attention in this paper is the relatively smooth surface of the woody endocarp in contrast to the ribbed or winged stones found in the fruits of other members of the genus. Two styles are present,

⁷ Some authors refer to "a bract and two bracteoles"; however a thorough comparative morphological study of the nyssaceous inflorescence has not yet been undertaken; therefore the present author prefers to use "bract" as a general term for all these subtending appendages, regardless of their apparent rank.

but one or both may be broken off from herbarium specimens. As a result, the styles were formerly described as solitary. When the first intact specimens were encountered, they were described as a new species, *N. bifida* Craib. This species was later treated as a synonym of *N. javanica* in Wasscher's (1935) revision of *Nyssa* in the Netherlands Indies. Other synonyms of *N. javanica* are *N. sessiliflora* Hook. f. & Thoms. and *N. arborea* Koord. Further details of description and synonymy may be found in Wangerin's monograph (1910) and in Wasscher's revision (1935, 1948).

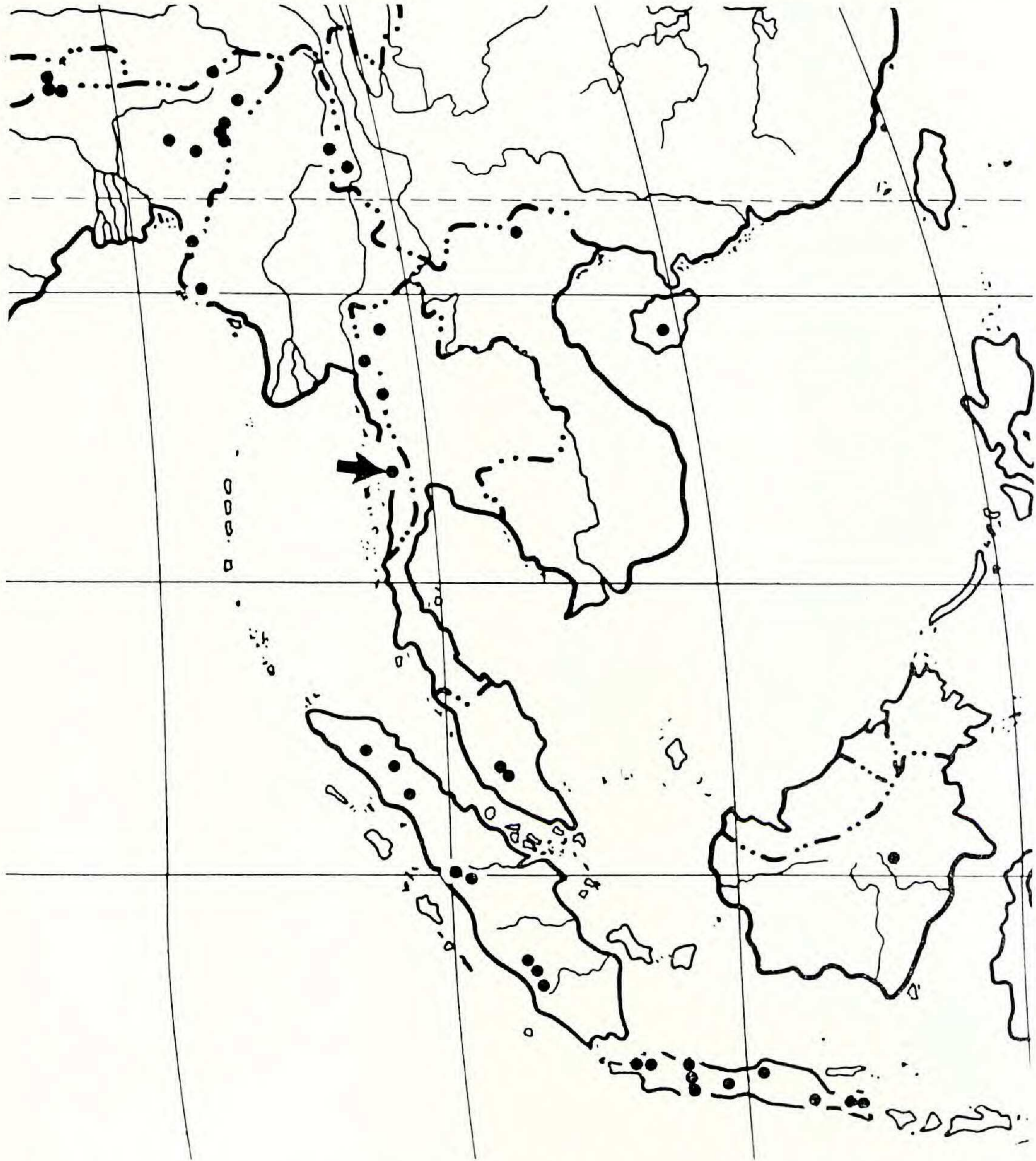
Prior to the publication of Wasscher's treatment, Parker (1929) attempted to separate the Indian nyssas into three species. His distinction between *N. javanica* and *N. bifida* is no longer tenable, but special interest attaches to his *N. megacarpa*. This name was based on three specimens, one bearing extremely large fruits (*Parker 2308*, collected "on Nwalabo at 1050 m.," Tavoy District, Burma). The species was said to differ from "*N. bifida*" not only in the size of fruits, but in the relatively glabrous appearance of the underside of the leaf and the fewer number of lateral nerves; a very slight difference in the length of staminate pedicels was also mentioned. All of these supposed specific differences described by Parker are well within the range of variation for *N. javanica*, except for the size of the fruits on his Tavoy specimen. With regard to the shape and markings of the endocarp and the outward appearance of the skin, these fruits are like any *N. javanica* fruits, but they are at least twice as large as most, and more than three times as large as some. Unquestionably they are the most massive modern *Nyssa* fruits that are known, and are the basis of references which have sometimes been made to "*Nyssa megacarpa*" in papers dealing with large fossil fruits of Nyssaceae. It would be more correct if reference were made instead to "*Parker 2308*" in order not to obscure the fact that the unusually large fruits were all taken from one tree.⁸

Parker was not the first to observe that some fruits of the *Nyssa javanica* type are larger than others. Koorders and Valetton (1900; p. 98, 101) reported that there were among the fruiting specimens of "*N. sessiliflora*" collected by Koorders at Takoka, in Java, a few that bore fruits of twice the usual size. Koorders and Valetton explained that the large-fruited specimens and the more plentiful small-fruited specimens were indistinguishable with regard to their foliar characters; otherwise they might have been treated as distinct species. Perhaps future botanical investigation based on larger collections will permit the confident recognition of varieties or even closely related species within the complex now known as

⁸ There are duplicates of *Parker 2308* in the Kew herbarium and in the herbarium of the Arnold Arboretum. One of two fruits accompanying the Kew sheet was removed for study by Kirchheimer, and photographs of the endocarp appear in some of his publications (1943, 1957). There were three additional fruits with the Arnold Arboretum sheet, the endocarp from one of which is now in the paleobotanical collection of Harvard University. The two other specimens cited by Parker in his description of *Nyssa megacarpa* (*Lace 4634*, *Kurz 1562*) are staminate flowering branches.

N. javanica; for the present, however, it seems preferable to deal with *N. javanica* as one very variable species.

Within the monsoon region, *Nyssa javanica* is widely distributed (MAP 4). Tall trees (reported up to 40 meters) of this species are found in wet montane forests of Sikkim, northern Bengal, and Assam; westward into Yunnan, Kwangsi and Hainan; and southward through mountainous parts of Burma, Thailand, Malaya, Borneo, Sumatra, and Java; thus *N.*



MAP 4. Distribution of *Nyssa javanica*. Arrow indicates locality where "*N. megacarpa*" was collected. (Copyright 1939, Goode Base Maps.)

javanica is the only species in the family to reach the equator. Herbarium labels indicate that the species can occur at a wide range of altitudes. Koorders and Valetton (1900) stated that it could be found all over Java at elevations of 700–1300 meters, but they reported some localities as low as 100 meters. Collections from the eastern Himalaya are often

taken from levels of 1500–2000 meters. Throughout its range this species grows under conditions of high humidity and very high seasonal rainfall to which other species of *Nyssa* are not exposed. Bor (1938) described a forested region just east of Bhutan in which *N. javanica* is present. He listed *Nyssa* as a dominant member of a “*Phoebe-Beilschmiedia-Engelhardtia* formation,” a type of evergreen subtropical forest with numerous lauraceous trees, occupying elevations of 1200–2000 meters between a lower tropical forest and a higher temperate forest. Bor estimated the annual rainfall at this level to be 4000–5000 mm. (p. 134). Temperatures are said to be equable and humidity high; “frost is not unknown.” Cowan (1929) described similar wet subtropical forests near Sikkim where *N. javanica* is associated with *Engelhardtia*, *Castanopsis*, *Schima*, *Betula*, and many other trees.

Trees of this species were examined by the author in a forest near Darjeeling, West Bengal. At an altitude of about 1500 meters, *Nyssa javanica* was fairly common, but widely scattered, and the individual trees would have been quite difficult to locate except for their lustrous, light green foliage, occasionally tinged with red, that set them off from other, darker canopy trees. Although the blades were fully expanded, it is likely that these leaves were still relatively new; this species, unlike most of its forest associates, undergoes a brief seasonal loss of foliage even in the southern part of its range (Koorders and Valetton, 1900). The crowns were high up on straight clean boles, making the collection of specimens rather difficult. Many of the upper branches left the trunks almost at right angles, reminiscent of *N. sylvatica*; the trees also resembled *N. sylvatica* in the appearance of the bark, which was light gray in color and divided into patches by numerous cracks, and in the frequent growth of sprouts from the bases of trunks. According to Gamble (1902), this species was once “in considerable use” in the Darjeeling Hills as a building timber; however the native collector who accompanied the present author asserted that it has no value now except as firewood and as “grass for cows” (i.e., branches are lopped off, and the foliage fed to domestic animals).

NYSSA AQUATICA Linnaeus. This is a very well-marked species, easily distinguishable from other nyssas by means of floral and foliar characters. The leaves are larger than those of the *Nyssa sylvatica* complex and there are coarse, mucronate teeth irregularly distributed along many of the leaf margins, a character not nearly so common in other American nyssas, and rarely, if ever, seen in the Asiatic species. Staminate flowers are in heads and hermaphrodite flowers are solitary. The hermaphrodite flowers develop into fruits differing in certain respects from any others in the genus, a matter to be taken up later in this paper.

In its distribution and habitat, *Nyssa aquatica* (MAP 5) is very similar to *N. biflora*. The two species frequently occur together in swampy regions of the Coastal Plain as far north as the Dismal Swamp in Virginia. *Nyssa aquatica* is the more common of the two, however, on the flooded alluvial plains of the Mississippi River, its major tributaries, and other south-

eastern rivers. *N. biflora* is more characteristic of acid coastal "pinelands" (Braun, 1950; Penfound, 1952). Applequist (1959b) has studied statistically the relationship between soil and site factors and the growth of both species. Forests composed almost entirely of *N. aquatica* are not unknown (Penfound and Hall, 1939), but more often *Taxodium* is present as a major associate. Although the trees thrive in standing water, it has been shown that periodic droughts are necessary for the continuation of this type of forest; seeds of *Nyssa* and *Taxodium* may survive long periods of submergence (Applequist, 1959a), but germination does not occur, nor are seedlings established, under water (Shunk, 1939; Demaree, 1932).

With a maximum height of 110 feet (Dixon, 1961), *Nyssa aquatica* is the tallest of American species of the genus. In dense stands the trunks are clear for two-thirds their height, and the crowns are quite narrow. In standing water these trees may develop a peculiar arching root growth as well as swollen bases.

NYSSA OGECHE Marshall. Although *Nyssa ogeche* has several characters in common with *N. aquatica* — relatively large leaves, capitate staminate inflorescences, solitary hermaphrodite flowers, and the swamp habitat — the two are easily separable in either the flowering or fruiting condition. The flowers of *N. ogeche* are covered with a dense tomentum and the fruits are borne on very short hairy peduncles. Leaves of this species are perhaps the most variable in the genus. On a single herbarium sheet one may find broad leaves oval to elliptic in outline, along with narrow oblanceolate leaves, and others with somewhat cordate bases. The leaf margins are usually entire, but the narrower leaves are sometimes toothed, especially on sprouts, which are very plentiful in this species. Leaves with tapering bases and rounded mucronate apices are perhaps most common. The hairy covering on young leaves is longer persistent in *N. ogeche* than in other species, and the underside of a mature leaf usually bears numerous unbranched trichomes, particularly along the midveins.

Nyssa ogeche, limited in distribution to eastern Georgia, northern Florida, and the southernmost part of South Carolina⁹ (MAP 5), has by far the most restricted range of any firmly established species of *Nyssa*. Within this limited geographical area, the species is locally abundant, appearing in swamps and along streams in the form of small trees less than 10 meters high, the smallest in the family, or shrubs with several stems. *Nyssa ogeche* is commonly associated with *Taxodium* and with *N. biflora*, but not so often with *N. aquatica*. The reason for this has not been established; however Oertel (1934) presented some data indicating that *N. aquatica* is often found in less acid soils than the other aquatic nyssas. Along the banks of the lower Chipola and Apalachicola rivers, the growth of *N. ogeche* is sufficiently dense to provide a major source of nectar to commercial apiaries, even though the flowering season for this species lasts no more than two weeks (Wood, 1958; Rahmlow, 1960a, 1960b). Because of the

⁹ In addition, the U.S. National Herbarium has one specimen collected at Mobile, Ala., by C. Mohr (*s.n.*) in 1890.

value of this species to beekeepers, the Agricultural Extension Service of the State of Florida has, in recent years, encouraged the planting of thousands of seedlings at appropriate sites in western Florida (personal communication from J. D. Haynie, Extension Apiculturist, Gainesville).

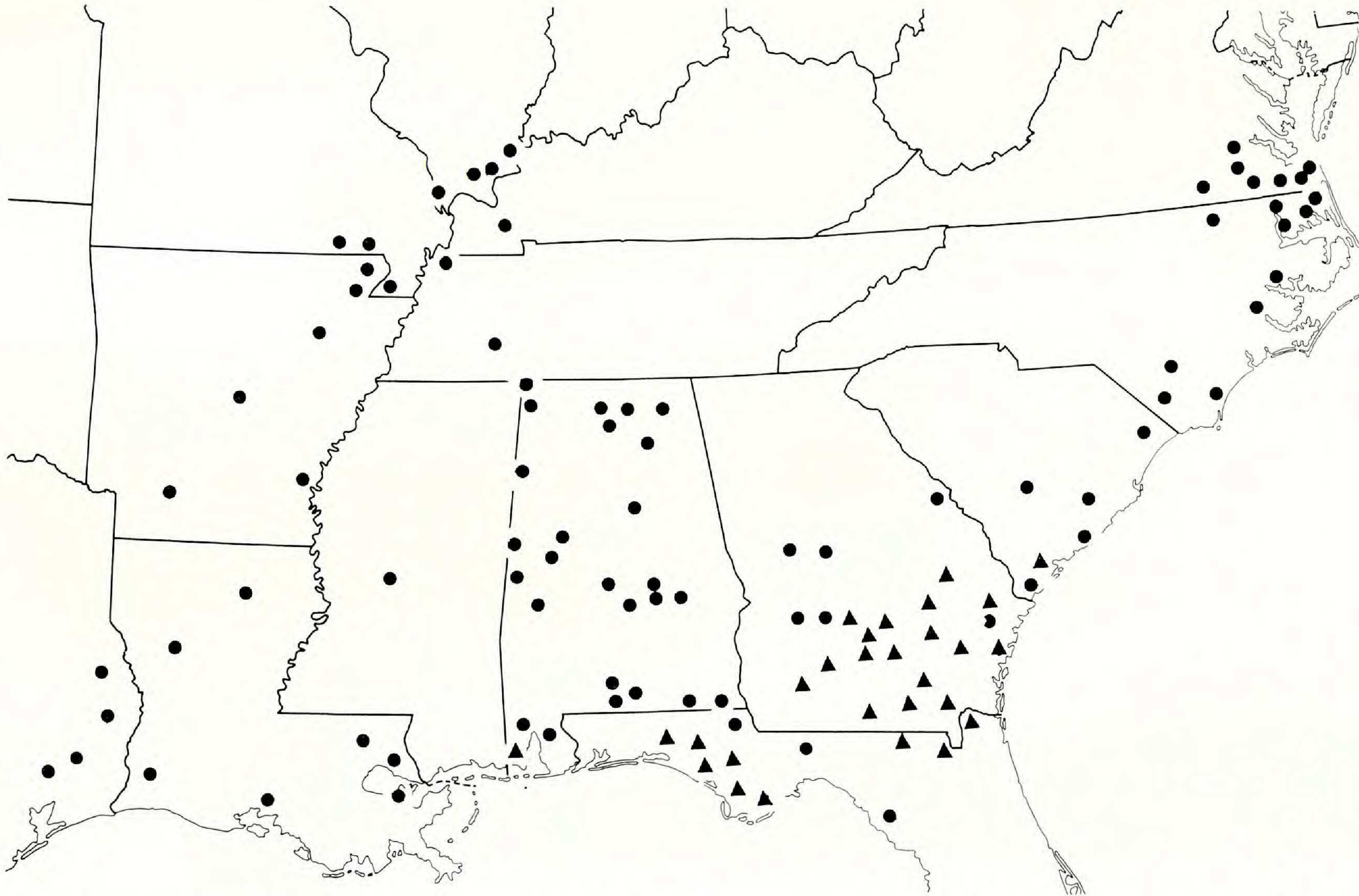
Comment must be made here regarding the name *Nyssa acuminata*, which Small (1903) applied to shrubby plants of coastal Georgia, believing them to be a different species from *N. ogeche*. Small listed the shrubby habit, narrower leaves, and smaller fruits of these plants as distinguishing characters. Later Eyles (1941) examined Small's collections of *N. acuminata* and compared them with other collections from the same general vicinity (between Warsaw and Townsend, McIntosh County) and from other parts of Georgia. As a result of these comparisons, Eyles concluded that Small's *N. acuminata* did not differ enough to be considered a species and that it might better be treated as a variety of *N. ogeche*. Small's type specimens were again examined as a part of the present study, and the problem of *N. acuminata* was kept in mind during the field work. At several places in western Florida shrubby growth agreeing in all characters with *N. acuminata* was found intermixed with and intergrading with trees of indisputable *N. ogeche*. Therefore, the author prefers to regard *N. acuminata* as falling within the range of variation of *N. ogeche*, rather than as a distinct entity.

Camptotheca and Davidia

Both of these genera were discovered by Father Armand David during his second major journey of exploration in China (1868 to 1870). The first collection of *Camptotheca* was made on Lu-Shan, in northern Kiangsi,¹⁰ and *Davidia* was later found in western Szechuan. Only one species is maintained in each genus.

CAMPTOTHECA ACUMINATA Decaisne. The leaves of this species have entire margins and acuminate tips, and are very variable in size. Specimens can be found to match either *Nyssa sylvatica* or *N. aquatica* in dimensions and outline. The globular capitate inflorescences may be solitary, or there may be two to several on branching stalks. The distal head in the branching system is composed of hermaphrodite flowers and is the first to mature. Judging from the appearance of fruiting herbarium specimens, the other, proximal branches of the system drop off as fruits ripen at the distal end, leaving a single cluster of fruits attached to one crooked stalk. The heads are very dense with sometimes more than 50 flowers and a greater number of hairy bracts tightly crowded together. It is surprising that almost all the flowers in many of these heads set fruit. The flat elongated fruits, often described as subsamaroid, are in marked con-

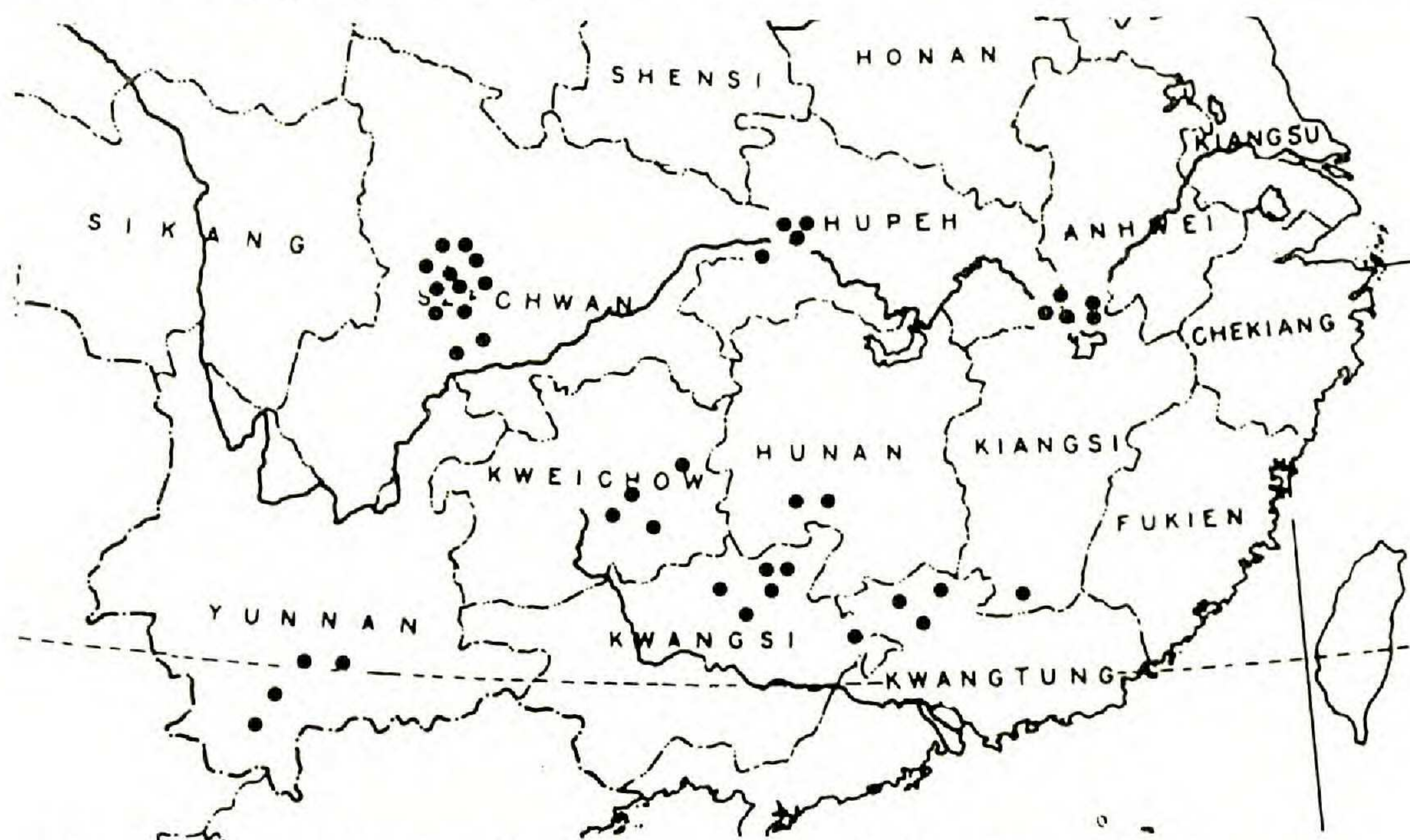
¹⁰ In the original description of *Camptotheca*, Decaisne (Bull. Soc. Bot. Fr. 20: 157. 1873) gave Tibet as the type locality. This error was subsequently corrected by Franchet (Plantae Davidianae 1: 357. 1884), a correction that passed unnoticed by Harms (1898) and by Wangerin (1910).



MAP 5. Distribution of *Nyssa aquatica* (circles) and *N. ogeche* (triangles). Several Alabama localities for *N. aquatica* taken from Harper (1928, p. 284); all others based on author's herbarium studies.

trast to the oval fruits of other Nyssaceae. This character is used as a major distinction in keys to the family. Markedly conical anthers and the occurrence of three styles are other distinctive characters of *Camptotheca*.

Since Father David's first collection in Kiangsi, additional collections have been made in that province and in Hupeh, Szechuan, Kweichow, Hunan, Yunnan, Kwangsi, and Kwangtung (MAP 6). According to Wang (1961, p. 106), *Camptotheca* also occurs at Tientai-Shan in northern Chekiang, a locality from which *Nyssa sinensis* has been reported. A comparison of the distribution maps shows a great similarity in the geographic ranges of *N. sinensis* and *Camptotheca acuminata*. Wang (p. 237) has listed *Camptotheca* together with *Nyssa* as a constituent genus of the mixed mesophytic forest formation. However, notes on herbarium labels show that *Camptotheca* is generally restricted to lower altitudes than *N.*



MAP 6. China, showing distribution of *Camptotheca acuminata*.

sinensis. In the Gray Herbarium and the herbarium of the Arnold Arboretum there are no specimens of the latter species for which an altitude below 500 meters has been noted; whereas collections of *C. acuminata* from levels below 500 meters are common. One may conclude from the data available that *Camptotheca* does not usually grow above 1000 meters except in Yunnan, where it may reach 1800 meters. Within this altitudinal range, it is found in wooded areas, sometimes attaining a height of 25 meters, or along open streams, frequently growing in thickets. Because of its rapid growth and regeneration, *Camptotheca* is widely planted in China beside irrigation ditches, and its branches are used for firewood (conversation with Dr. S.-Y. Hu). The Chinese also cultivate it as an ornamental (Steward, 1958).

DAVIDIA INVOLUCRATA Baillon. The foliage of *Davidia involucrata* bears little resemblance to that of other Nyssaceae. The leaves are cordate with serrate margins, long slender petioles, and prominently branching venation

approaching the palmate condition. Pendulous flowering heads are produced on short lateral shoots along with a few leaves. These heads are solitary on long peduncles, on which there are also two (sometimes three) large, white, unequal bracts. The bracts, in contrast to the foliage leaves, are sessile, membranaceous, and most often without marginal teeth. An inflorescence is made up of numerous closely united staminate flowers, devoid of sepals and petals and giving the appearance of a single flower bearing hundreds of stamens. The stamens, purple in color and quite long, make a very striking display in combination with the white bracts. Solitary hermaphrodite flowers arise from otherwise staminate inflorescences. These flowers are of considerable importance to any comparative study of nyssaceous fruits because they retain an apparently primitive multilocular condition.

Although *Davidia* is also a genus of the mixed mesophytic forest formation, it is mostly confined to elevations of 1600–2500 meters and is consequently not found in the lower Yangtze region. In the upper Yangtze area it is sometimes locally abundant; Wang (1961, p. 112) describes a forest in eastern Szechuan in which *Davidia*, *Euptelea*, and *Fagus* are the most plentiful elements. *Davidia* has also been collected in western Szechuan and from localities in Hupeh, Kweichow, Sikang, and western Yunnan (MAP 7). In the latter province it reportedly reaches an altitude of 3000 meters. In its native habitat, *Davidia* grows to a height of 20 meters, with about 10 meters of clean trunk below the crown. (Cultivated in the open, it assumes an attractive pyramidal form.) When these trees are in bloom, the fluttering of their white bracts in the forest canopy is said to be an extremely attractive sight. E. H. Wilson, who on several occasions observed the flowering of *Davidia* in the Chinese forests, and who played the major role in its introduction to western gardens, wrote (1913): “To my mind *Davidia involucrata* is at once the most interesting and beautiful of all trees of the north-temperate flora.”

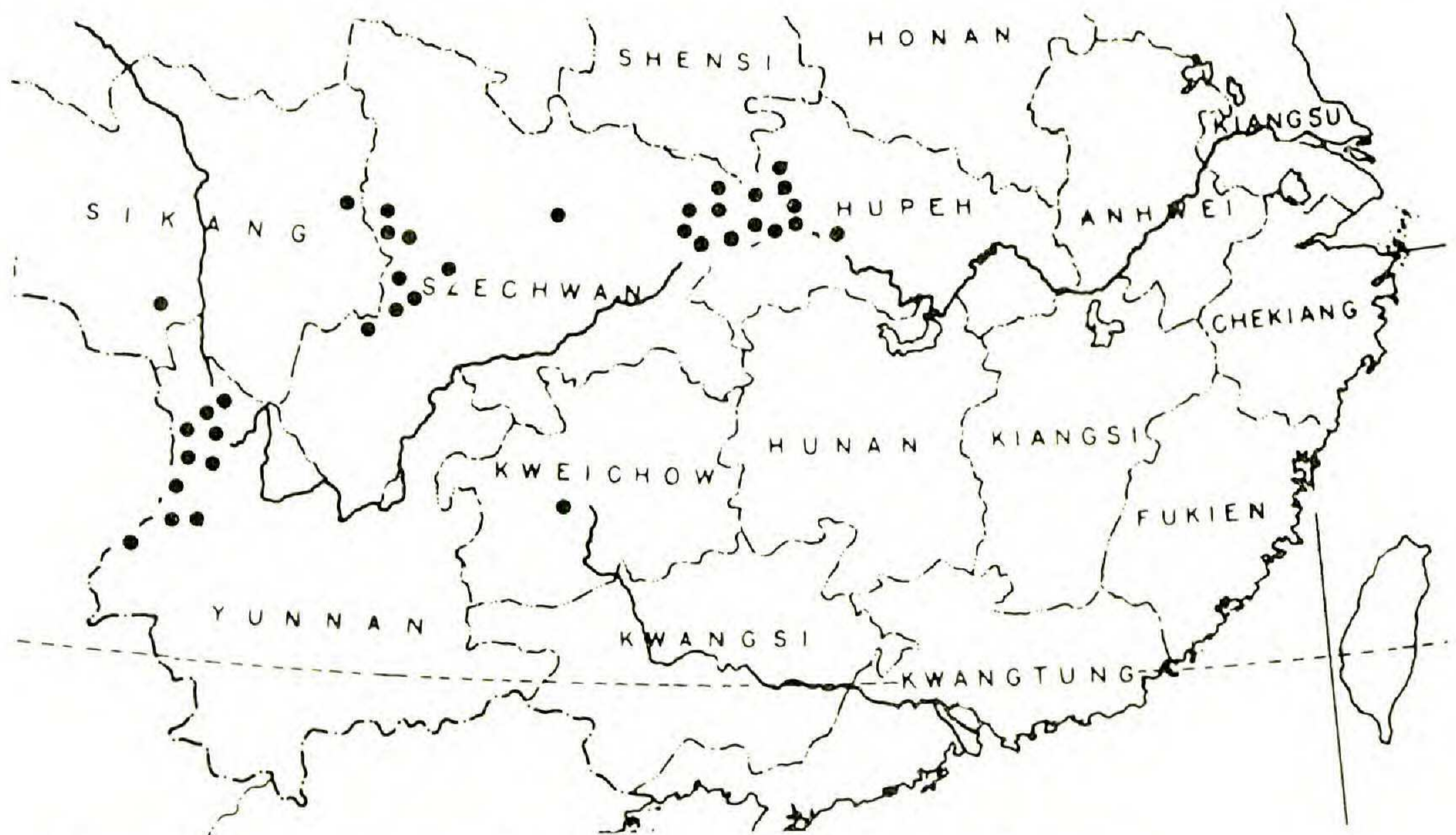
The taxon *Davidia involucrata* var. *vilmoriniana* (Dode) Wangerin¹¹ includes those individuals bearing glabrous mature leaves, as distinguished from the hairy-leaved type originally collected by Father David. The typical variety and var. *vilmoriniana* have been observed growing together in the wild state (Bean, 1950), but the latter is said to be more hardy.

The Genus *Mastixia*

No attempt to deal with individual species of *Mastixia* Blume will be made here: systematically the genus is still not very well known, and some of the putative species have been collected only once or twice. Danser (1934) listed nine species in his revision of the Cornaceae of the Netherlands Indies; no doubt there are additional species growing in other parts of the *Mastixia* range, but the total number probably would not exceed 15.

Members of this genus are evergreen trees 10–35 meters tall with typical

¹¹ This name has been cited “var. *vilmoriniana* (Dode) Hemsley” by most authors, but Wangerin’s (1910) combination antedates Hemsley’s (1912).



MAP 7. China, showing distribution of *Davidia involucrata*.

rain forest leaves — leathery blades, entire margins, and prominent acuminate tips. Both alternate and opposite arrangements are common, often on the same plant. The flowers are all hermaphrodite, borne in many-branched, often trichotomous, panicles with a bract at each node. The anatomy of the *Mastixia* stem is of special interest with respect to the phylogeny of the Umbellales: secretory canals are present in the pith, suggesting a relationship with the Araliaceae, and the vessel members are of a very primitive type.

The distribution of *Mastixia* has been discussed in detail by Kirchheimer. His map (1943, p. 17) of the range of this genus includes northern New Guinea, Indonesia, and the Philippine Islands; the southeast Asiatic mainland from Malaya north to Vietnam and the eastern Himalaya; also Ceylon and the southern part of the Indian peninsula. There are other localities of which Kirchheimer was not aware in the Solomon Islands (Merrill and Perry, 1940, p. 527); Yunnan (Merrill, 1937); and Hainan (Merrill and Chun, 1940, p. 153). Many of the collections have been made in wet tropical highlands at elevations up to 2000 meters (a comparison of collectors' notes reveals that some of these were found in the same forests with *Nyssa javanica*). Kirchheimer has pointed out, however, that some species of *Mastixia* are more characteristic of lowland rain forests, and that these species may be encountered near equatorial coasts as well as on higher ground; in this respect, *Mastixia* is unique among the Cornaceae.

MORPHOLOGY OF THE FRUITS

Laboratory Methods

Endocarps were prepared for gross examination by boiling in water or in dilute caustic soda to remove the outer fleshy layers of the fruit. Microtome sections were used for the finer observations. Before sectioning it

was necessary to soften the woody tissues by soaking for a week or longer in hydrofluoric acid. The specimens were imbedded in celloidin (Mallinckrodt's "Parlodion") whenever it was desirable to include softer parts of the fruit in the sections. Procedures for imbedding in celloidin may be found in a paper by Wetmore (1932) and in standard manuals on micro-technique. Some of the fruits, especially those picked when not fully ripe, did not soften much, even after prolonged soaking in HF, and sections were cut with considerable difficulty; however such sections were adequate for the study of cellular arrangement and vascular patterns, even if they were not always as pleasing a subject for photographic presentation as one might have desired. Sections were cut at various thicknesses, depending upon the hardness of individual specimens, but most sections were cut at 20–30 μ . The celloidin method does not yield a continuous ribbon of serial sections; each slice must be handled separately, a rather laborious procedure; therefore complete series were maintained only for regions of particular interest within the fruit, such as the placental region. From other parts of the fruit only every third or fifth section was taken, depending upon the size and importance of the specimen. Staining with iron alum and hematoxylin was carried out in individual Syracuse watch glasses whenever necessary; frequently enough detail could be seen in sections of mature fruits without staining.

Initial observations on mature fruits raised morphological questions that could be answered only by examining younger material. Flowers of all species and young fruits of *Nyssa sylvatica* were dehydrated with a butyl alcohol series, imbedded in "Tissuemat," and sectioned on a rotary microtome. A number of different staining procedures were used but Popham's schedule for staining shoot apices (Popham *et al.*, 1948) yielded very pleasing results.

Flowers and young fruits were also studied after bleaching and clearing whole specimens. Sodium chlorite proved to be an effective bleaching agent (Barghoorn, 1948), and material treated with this compound could be cleared quite easily by transferring subsequently to water, chloral hydrate, alcohol, and finally xylene or toluene for appropriate intervals (Arnott, 1959). Vascular patterns in flowers were visible at low magnifications after this method had been applied; in developing fruits the extent of lignification of the endocarp could also be seen through the transparent outer fleshy layers. Flowers of some species had a dense coating of epidermal hairs that obstructed the view of internal features, and it was then necessary to tease the surface with a camel's-hair brush before any observations could be made. It was found that flowers could be imbedded in paraffin and sectioned in the usual manner even after clearing, and some of the specimens were studied by both of these methods.

Fruits of the *Nyssa sylvatica* Complex

The mature drupe of *Nyssa sylvatica* and closely related forms is blue-black in color and about one centimeter long. It is usually ovoid, but in

unusual cases — e.g., the *N. ursina* fruit — it may become quite globular. At the apical end is a wrinkled pulvinate disk one to two millimeters in diameter, a scar in a depression at its center marking the former location of the style. Surrounding the disk is the calyx rim with five indistinct teeth. At the base of the fruit there are one to three inconspicuous hairy bracts, the largest of which is about a millimeter long; these remain attached to the peduncle when the fruit falls.

Removal of the outer fleshy layers of the drupe reveals a fibrous woody stone with 9 to 12 vascular bundles situated in longitudinal grooves, the areas between the bundles standing out as rounded ridges. The dorsal (abaxial) side is flattened, the ventral side convex when only one locule is present; bilocular endocarps are a little flattened on the dorsal side of each locule, with the lateral margins somewhat convex. There is one anatropous seed ventrally attached near the apex of each locule with its extrorse micropyle directed upward. The embryo is straight, and its radicle is directed toward the micropyle. During germination the rapidly elongating radicle ruptures the thin seed-coat and pushes open a triangular germination valve at the apical end of the endocarp.

Bilocular endocarps are extremely rare in American members of the complex. Kirchheimer found one, photographs of which appear in one of his papers (1948, *fig. 4b & c*), in a collection of 200 fruits from plants of *Nyssa sylvatica* escaped from cultivation in Germany. In a later publication (1957, p. 571), he stated that about two per cent of the endocarps of this species are bilocular, without offering any further explanation. In the opinion of the present author, bilocular endocarps of *N. sylvatica* are far less common than Kirchheimer's estimate would indicate. During this investigation, the bilocular condition was not found in mature fruits of any American members of the complex, even though hundreds were examined. The condition would not be difficult to detect, because bilocular endocarps are thicker and have two germination valves. Herbarium sheets were examined closely in a search for flowers with two styles — in *N. sinensis* this is an indication that two locules are present — but such flowers were found only twice during the entire study. In one case the flowers are obviously abnormal: the specimen (*Fernald & Long 11599*, GH) was found flowering in the vicinity of the Dismal Swamp, Virginia, on October 12th.¹² Its incompletely developed inflorescences bear several malformed flowers as well as some apparently normal ones with two styles. Clearing one of the better flowers from this specimen revealed a bilocular ovary. In *N. sinensis*, on the other hand, two styles accompanying bilocular ovaries are present in perhaps a third of the hermaphrodite flowers. These ovaries develop into bilocular fruits with two seeds; the author has not found a fruit of *N. sinensis* in which one of two ovules has failed to develop

¹² The author has seen cases of late-summer flowering in the Okefenokee Swamp (*Nyssa biflora*), and within the shrubby *N. ursina* thickets of the Apalachicola River delta, where such flowering is not at all uncommon. However, in every instance observed by the author, only staminate plants were flowering; at the same time, fruits were maturing on adjacent hermaphrodite plants.

or in which one locule is notably larger than the other. Kirchheimer (1948, p. 94) stated that trilocular fruits are produced occasionally by *N. sinensis*; however trilocular fruits were not found either in this species or in any modern *Nyssa* during the present investigation. It is possible that Kirchheimer erred on this point.

Examination of herbarium specimens gives the impression that fruits of *Nyssa sinensis* and *N. biflora* (exclusive of *N. ursina*) are somewhat larger than those of *N. sylvatica*. In order to test the significance of apparent size differences, a large fruit was chosen from each of 44 dried *N. sylvatica* specimens in the herbarium and its length measured with vernier calipers. Similar measurements were obtained from 44 specimens of *N. biflora* and from 41 specimens (all of the mature fruiting specimens in the Harvard collections) of *N. sinensis*. Some of the difficulty involved in separating specimens of *N. sylvatica* from those of *N. biflora* was avoided by using only those specimens of *N. sylvatica* collected outside the *N. biflora* range. Thus the measurements include a geographical bias as well as a bias in favor of larger fruits. Only length measurements were taken, because measurements of breadth or thickness of whole fruits are of little value once the outer layers of the fruit wall have been pressed flat on herbarium sheets; and experience shows that the longer fruits are usually larger in other dimensions as well. The ranges in fruit-length for the three species were: *N. sinensis*, 8.0–14.2 mm.; *N. biflora*, 8.1–12.3 mm.; *N. sylvatica*, 7.5–12.8 mm. The respective means were 10.4 mm., 10.3 mm., and 9.6 mm. Application of the “*t*-test” showed that the mean measurements for *N. sinensis* and *N. biflora* each differed significantly from the *N. sylvatica* mean (*N. sylvatica* vs. *N. biflora*, $P = .05$; *N. sylvatica* vs. *N. sinensis*, $P = .01$). If one assumes that the selection of a single large fruit from each herbarium sheet yields a sample to some extent representative of the species, it may then be inferred from the data that the fruits of *N. sinensis* and *N. biflora* are, on the average, larger than those of *N. sylvatica*.

Fruits of the putative species *Nyssa ursina* are the smallest in the complex. These are mostly the same size (7.5–10 mm. long) as the smaller fruits of *N. sylvatica* and *N. biflora*.

SIZE OF ENDOCARPS. Removal of the fleshy outer wall and apical disk from a dried fruit reduces the length by about a millimeter. The longest apparently normal endocarp encountered in the complex came from a bilocular *Nyssa sinensis* fruit 14.2 mm. long; it measured 13.1 mm. after boiling and drying, with a breadth of 6.3 mm. in the plane of symmetry between the locules and a thickness of 5.3 mm. across the locules. Broader (up to 7.4 mm.) and thicker (5.5 mm.) endocarps have been found in both *N. sylvatica* and *N. biflora*. The smallest endocarp seen during the entire investigation came from *N. sylvatica* from Martha's Vineyard (*F. MacKeever MV306*, NEBC); it is 4.4 mm. long, 4.1 mm. wide, and 3.2 mm. thick. Some abnormally long and thin specimens were obtained from *N. biflora* collected in the Okefenokee Swamp (*A. Traverse 498*, GH); the

dried fruits are 15 mm. in length with endocarps up to 14.3 mm. long and only 3 mm. thick.

Variation in stones of the *Nyssa sylvatica* complex is shown in PL. I, FIGS. 3 and 5.

HISTOLOGICAL OBSERVATIONS. Cross sections of a mature fruit reveal an outer thick-walled skin of six to ten cell layers separated from the woody stone by a much wider succulent zone of large, thin-walled cells. Sclereids, solitary or in clusters, are present in the transition region between these outer tissues. The transition between fleshy tissue and endocarp¹³ is marked by a few layers of small cells that are rectangular in outline and not nearly so heavily lignified or thick-walled as the fibrous elements of the endocarp. In selected sections, and in sections of younger material (PL. III, FIG. 15), it may be seen that the fused vascular bundles supplying both carpels and epigynous floral appendages are within this transition region. It may be properly called a "zone of adnation," joining the carpellary (woody) tissues with the surrounding fleshy tissues of the hypanthium. The endocarp in the species of the *Nyssa sylvatica* complex (and in other species of *Nyssa*) is made up almost exclusively of thick-walled fibers, 200–700 μ in length and 15–25 μ in diameter, with very small lumina. In the immediate vicinity of vascular bundles these are elongated in the same direction as the vascular elements; otherwise, the outermost fibers are transversely oriented, forming a sinuous pattern in conformity with the alternately ridged and grooved surface of the stone. The innermost cell layer — the inner epidermis of the carpel — is composed of longitudinally elongated fibers which become separated in places during expansion of the fruit. Locally some of the fibers adjacent to (and derived from ?) the inner epidermis may also elongate longitudinally, but this phenomenon is mostly confined to the one layer of cells. Almost everywhere, throughout the length of the endocarp, the cell layers immediately external to the inner epidermis are made up of transverse fibers, circumferentially elongated in conformity with the outline of the locule. Between this circumlocular zone of transverse fibers and the less distinct zone of transverse fibers near the periphery of the endocarp, the elements are chaotically arranged. No order is discernible in the chaotic region, except that the fibers are often parallel within aggregates of 20 to more than 50 elements. Similar aggregates are found in the stones of all *Nyssa* species. When Kirchheimer stated (1938, p. 2) that there are "nests of stone-cells" within the *Nyssa* endocarp he probably had observed some of these aggregated fibers cut transversely; the present author has found no nests of

¹³ The terms "exocarp" and "mesocarp" have been avoided here in keeping with Esau's recommendation (1953, p. 578) that they be used only in cases where the fruit wall is made up entirely of carpellary tissues. On the other hand, a loose usage of "endocarp" seems justified, since "endocarp" is universally employed in paleobotanical literature as a synonym for the woody stone of *Nyssa*. Moreover, "endocarp" is sometimes a more suitable term than "stone": the inner layers of the fruit wall may be called "endocarp" at any stage of development, but the term "stone" is applicable only at maturity, when this tissue has become sclerified.

brachysclereids, either by sectioning or by macerating the stones. There are, however, some individual strands of crystalliferous parenchyma cells visible in younger material, and these become heavily lignified along with the fibers when the fruit matures.

Orientation of elongating elements in a developing endocarp of *Nyssa sylvatica* may be seen in PL. IV, FIG. 20.

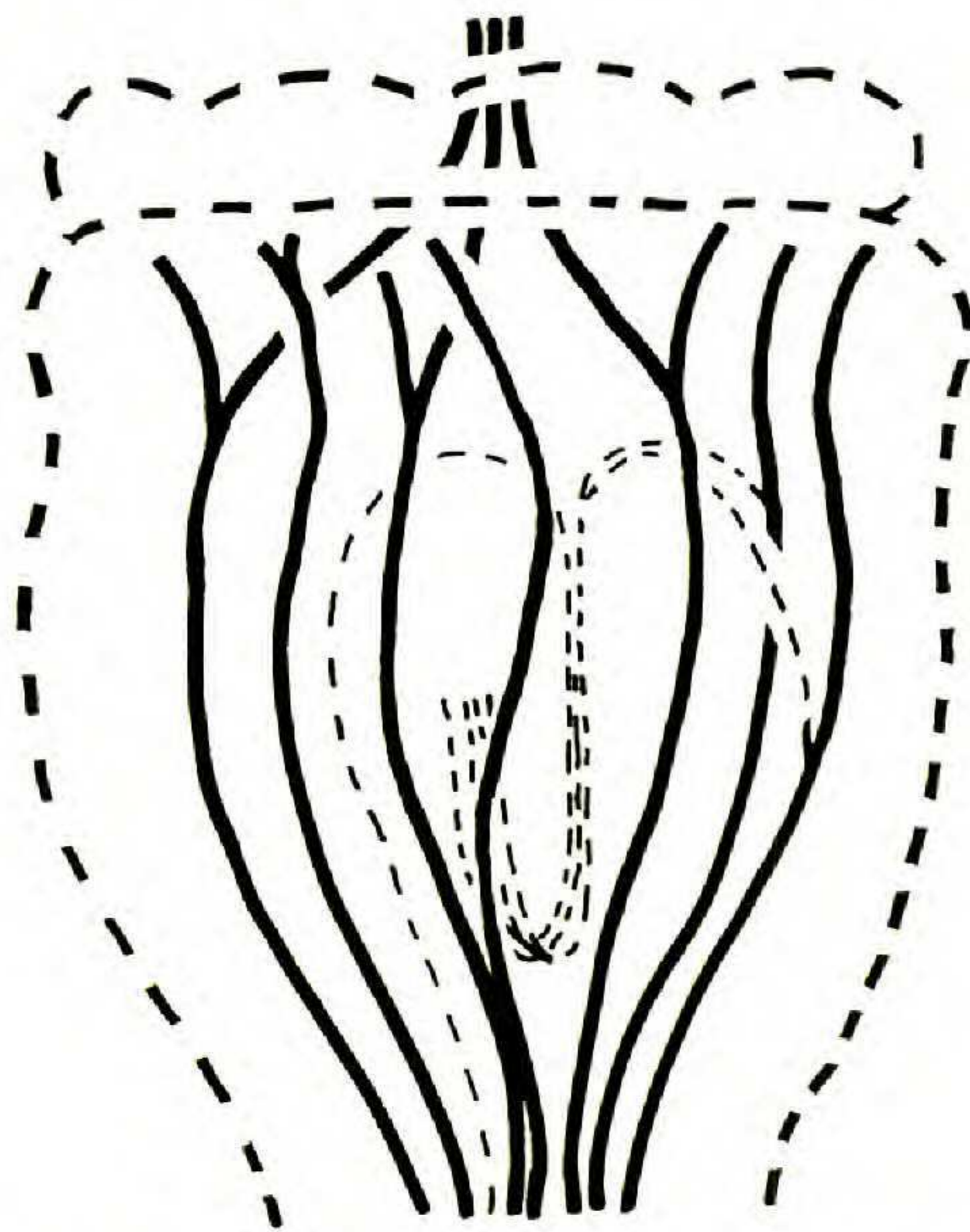
In transverse sections taken from the apical third of the fruit, the continuity of the fibrous tissue is interrupted by two narrow bands of smaller cells, somewhat rounded to elliptic in outline, marking the margins of the germination valve. These cells are neither as thick-walled nor as heavily lignified as the fibers, and they are very loosely united or even completely free from each other. Sections from a number of fruits show that the borders of the valve are completely free at maturity except for the cells of the adnation zone; these are easily ruptured during germination. It is possible to induce the germination valve to open in the laboratory by repeated boiling and drying. Subsequent microscopic examination of the valve margins reveals that the cells have been ruptured only in the outermost cell layers. The outer part of the margin has a ragged appearance after opening; whereas the inner part is relatively smooth. At its base the valve is continuous with the rest of the endocarp, but in this region transverse fibers are markedly predominant. The basal breaking of the valve during germination, consequently, occurs between fibers rather than across them.

The seed coat is thin and membranaceous, consisting of only a few crushed cell layers, all that remains of the thick integument to be seen in sections of flowers. In all nyssaceous species the cells in the outermost layer of the integument develop very thick, heavily lignified external walls that adhere tightly to the inner cells of the endocarp. The seed contains abundant endosperm tissue inclosing an embryo with well-developed cotyledons.

VASCULAR PATTERN. It is usually possible to identify the dorsal carpelary bundle of the endocarp with the unaided eye, for it occupies a prominent position in the center of the flattened dorsal side. Flanking this bundle, on either side, are two other bundles of similar size. The dorsal and its two flanking bundles lie closer together than most of the other bundles on the surface of the endocarp, and they are sometimes the only bundles to pass over the germination valve. This three-fold vascular pattern occurs often in Nyssaceae, making it possible to locate the dorsal side of the endocarp when other marks are not present, i.e., when the margins of the germination valve are hidden beneath the cell layers of the adnation zone and when dorsal flattening is not pronounced. Most of the details of the vascular system are no longer apparent once the endocarp has become woody. It is necessary, therefore, to examine flowers and developing fruits in order to understand the roles of the various bundles. In cleared preparations of very young specimens a ring of five vascular strands at the very base of the inferior ovary can be seen to branch at higher levels, to

become the 8 to 10 bundles supplying, alternately, the petals and the calyx lobes. (Hermaphrodite flowers of the *Nyssa sylvatica* complex are pentamerous for the most part, but tetramerous specimens may be found.) Just below the distal margin of the hypanthium, a bundle supplying a sepal usually connects with a staminal bundle; however, the stamens frequently are fewer in number than the calyx lobes. The style contains three prominent strands. The median strand of these three styler bundles is the dorsal carpellary bundle. The two lateral strands will be called ventral carpellary bundles in this paper, but it must be noted that the term "ventral" as used here does not necessarily indicate a connection with the ovular supply; it merely serves to designate the two major bundles that accompany the dorsal bundle into the style. In the present usage, "dorsal bundle" and "ventral bundle" will include both the basal part of the strand, where it is usually fused with a perianth bundle, and the apical part, where it is purely a carpellary bundle. Fusion of ventral bundles with the perianth supply is rather constant in the *N. sylvatica* complex, but the dorsal bundle occasionally is free of any connections along its entire length.

The ovular supply is visible within the ovary of a cleared flower taken at anthesis or later. A semidiagrammatic drawing of one such flower is shown in TEXT-FIG. 1. The stamens and petals have fallen away from the



TEXT-FIG. 1. Semidiagrammatic drawing of vascular system in cleared hermaphrodite flower of *Nyssa sylvatica*. External broken lines represent outline of hypanthium and disk; solid lines represent major vascular bundles; internal broken lines represent ovular supply. Further explained in text. See also PL. III, Figs. 14-16.

apical disk, and the long recurved style has broken off near its base. The ovary is viewed from its dorsal side, but it is turned a bit so that the ovular supply can be seen more clearly. The outline of the ovule is not visible and only seven of the perianth bundles are shown, the three bundles

farthest from the viewer having been omitted for the sake of clarity. There is a perianth bundle on each side of the dorsal, separating it from the ventrals (in most specimens the dorsal is separated from at least one of the ventrals by *two* bundles). These are the two flanking bundles that often pass over the germination valve of the mature endocarp in close association with the dorsal bundle. The ovular vascular supply in this specimen is not connected with the stelar vascular supply. This is usually the case in unilocular flowers of the *Nyssa sylvatica* complex; in more mature ovaries the ventral bundles also will provide branches into the placenta, but instances in which the ventral carpellary bundles provide the earliest and strongest supply to the ovule are rare. Another notable point regarding the ovular supply can be seen: the strands from one side are connected with perianth bundles, but the bundle entering the ovule on the other side does not connect with any other strands. This is not due to an omission in the drawing; in most unilocular ovaries there is at least one strong ovular trace that extends from the base of the ovary to the ovule without being fused to the perianth supply. In the mature fruit, such a bundle will lie in a groove at the surface of the endocarp for most of its length, entering the endocarp wall at about the same level as the base of the germination valve (PL. I, FIG. 4); hence, there are often more grooves and strands on the surface of the endocarp than there are perianth parts. When developing fruits are cleared just prior to thickening of the fibers, the ovular supply is even more complex; most of the perianth bundles — except the dorsal and its two flanking bundles — are connected with the placental region by one or more strands. These traces meet at the placenta and combine into one very strong strand which enters the integument and runs along the ventral side of the ovule to its base; there the strand separates into four or five anastomosing bundles that rise on the dorsal side of the ovule for more than half its length. At this advanced stage the vascular pattern of the ovary is further complicated by the appearance of additional weak bundles near the apex of the ovary; they are attached to the more ventrally situated perianth bundles and extend into the base of the style. These strands, ending blindly, could be interpreted as vestiges of the stelar supply of a second carpel.

Flowers with bilocular ovaries have two styles, each of which contains a dorsal and two ventral bundles. Each of the ventral traces has a common origin with the ventral from the other stelar branch; i.e., a pair of ventrals are fused at either side of the ovary, the two members of a pair belonging to different carpels. The fusion may be only at the base of the ovary, or it may extend for some distance, and the pairs of ventrals on opposite flanks of the ovary are usually not fused to the same degree. In addition, the carpellary bundles usually are fused to perianth bundles at the periphery of the developing endocarp. The two ovules are attached at either side of a septum — a partition in which the ventral portions of two carpels are united — that continues the length of the ovary. Two separate sets of ovular traces pass through the septum connecting the placentae with the ventral bundles and the one or two adjacent perianth

bundles. The ovular traces are not connected with so many perianth bundles as in the unilocular ovary, and those peripheral bundles that do connect with the ovular supply usually connect with more than one ovular strand. It is notable that in bilocular fruits more of the ovular strands are connected with ventral carpellary bundles than is the case in unilocular fruits.

The word "usually" must be employed liberally in a description of the complex vascular system of these inferior ovaries. When a large number of cleared specimens are examined (about 50 were inspected in preparing this description) the variability is most impressive.

ORIGIN OF THE GERMINATION VALVE. This investigation did not include an exhaustive study of histological changes at various stages of development, but enough material was examined to obtain some understanding of the origin of the valve. The presence of this peculiar structure is apparently due to the interaction of two different patterns of growth in the endocarp tissue: (1) the tendency of cells in the vicinity of developing vascular bundles to elongate parallel to the bundles; (2) the transverse elongation of other cells, particularly near the inner epidermis and the adnation zone, as the ovary increases in diameter. The initial position of the valve margin is established by the first of these factors; the second factor accounts for its final form. Cross sections through young flowers show that the upper part of the endocarp already contains the entire ovular supply, at least in the form of prominent procambial strands. The strands run obliquely, sometimes almost transversely, from the ventrally and laterally situated perianth bundles into the placenta, and a great many of the developing fibers in this part of the endocarp elongate parallel to them. Since there are no ovular bundles connecting with the dorsal bundle and at least two of the bundles closest to it, the developing fibers on the dorsal side retain a predominantly transverse orientation. Between the ventral region, where obliquely oriented cells predominate, and the dorsal region, where transversely oriented cells predominate, is a narrow zone of cells that do not elongate, nor do they enlarge and become thick-walled along with the other cells of the endocarp. It is these cells that form the line of dehiscence at the edge of the germination valve. As the fruit wall increases in diameter, more growth takes place on the ventral side of the locule than on the dorsal (hence the bundles on the ventral surface of the mature unilocular endocarp are more widely spaced than the dorsally situated bundles), and the line of dehiscence comes to occupy a more dorsal position.

When developing fruits are cleared just before thickening of the fibers, which renders the endocarp opaque, the relationship between the ovular supply and the position of the germination valve is apparent. In such preparations the line of dehiscence is just visible, arising from the same level as the major ovular bundles and following a similar curved path to the apex of the endocarp. Another indication of the relationship between the ovular supply and the germination valve may be seen on the dorsal surface of the mature unilocular endocarp: on each side of the valve, the basal terminus

of the line of dehiscence is usually contiguous to or closely associated with a bundle that is two bundles removed from the dorsal, i.e., a bundle that is adjacent to a flanking bundle; cross sections and cleared preparations of flowers show that this is commonly the most dorsally situated bundle with which an ovular bundle connects.

The basal terminus of the dehiscence line in bilocular endocarps is sometimes more closely associated with one of the flanking bundles. It may be that where there are fewer perianth bundles per ovule, the flanking bundles sometimes connect with ovular strands; bilocular fruits were not sectioned in sufficient number to verify this point.

Fruit of *Nyssa javanica*

It was not possible to examine fresh fruits of this species. Reportedly they are purple in color (Wasscher, 1948) and pleasantly acid to the taste (Koorders and Valetton, 1900). Corky spots are conspicuous on the dark-brown epidermis of dried specimens. The pulvinate disk has a pronounced stylar depression.

Cleaned endocarps are similar in shape to those of *Nyssa sylvatica*, but the apex is often more pointed, the outline of the germination valve is much more conspicuous, and above all, the surface is much smoother (PL. II, FIG. 10). There are no vascular bundles attached to the dorsal surface, but a distinct median ridge is present at the apex of the germination valve. This ridge diminishes at the base of the valve, then reappears as a less distinct median ridge extending to the base of the endocarp. To either side of the median dorsal ridge, and separated from it by a shallow longitudinal depression, is an indistinct ridge. The three ridges occupy the same position on the surface of the endocarp as the three most dorsally situated bundles of *N. sylvatica* and other *Nyssa* species, therefore, they will be referred to as the dorsal ridge and two flanking ridges. Additional inconspicuous ridges sometimes occur on the ventral surface of the *N. javanica* stone, and occasionally a sharper ridge is present on one or both sides. A few weak vascular bundles are usually visible on the ventral surface which arise at the base of the sides and extend only part of the way to the apex. Rarely, they are heavier and divide the ventral surface at its base into a few broad rounded ribs.

The ovaries of *Nyssa javanica* are unilocular, although they bear two styles. The outline of the locule of a mature fruit (PL. II, FIG. 11) coincides with the dorsal sculpturing of the stone: in the region below the valve there is a broad median dorsal groove flanked by two less conspicuous ridges; the ventral endocarp wall has a broad internal ridge, just opposite the dorsal groove. This is the only nyssaceous species in which internal sculpturing of the locule is evident.

The range in size of *Nyssa javanica* endocarps is very great. The smallest of 25 stones taken from 22 herbarium sheets measured 8.9 mm. in length, 6.2 mm. in breadth, and 4 mm. in the plane of symmetry; the largest was 17.8 mm. long, 10.9 mm. broad, and 6 mm. thick, the median length was

14.2 mm. These measurements do not include the remarkably large fruits collected by Parker (no. 2308) in Burma: there are two of Parker's fruits in the herbarium of the Arnold Arboretum (and one in the paleobotanical collection of Harvard University), in the largest of which (PL. II, FIG. 10) the endocarp is 29.8 mm. long, 15.2 mm. broad, and 8.2 mm. thick.¹⁴

HISTOLOGICAL OBSERVATIONS. The histological composition of the fruit wall of *Nyssa javanica* differs in several respects from that of *N. sylvatica*. One difference is the greater abundance of stone cells in the outer fleshy layers of the *N. javanica* fruit, a character that can be seen very well in cleared preparations. A more important difference is the more limited extent of the fibrous tissue in the *N. javanica* fruits, i.e., the woody layers do not extend to the peripheral ring of fused vascular bundles that marks the transition between gynoecium and hypanthium. Instead, several of the outermost cell layers within this ring — layers of carpellary tissue — remain fleshy along with the noncarpellary tissues; therefore, the major bundles are surrounded by parenchyma, and they separate quite easily from the endocarp when it is cleaned. The outer zone of transversely elongated fibers forming the grooves and ridges of the *N. sylvatica* fruit is lacking in *N. javanica*; instead there are large quadrilateral thin-walled cells in the outer carpellary layers. The innermost of these, just adjacent to the stone, have somewhat thicker walls; in cross sections of herbarium specimens they do not appear so crushed and torn as the outer cells. All of the large quadrilateral cells come away from the fibrous layers when the fruit is boiled, leaving the smooth-surfaced stone that is characteristic of this species.

The innermost layers of the endocarp (PL. V, FIG. 23) are similar to the corresponding layers in *Nyssa sylvatica*; a single epidermal layer of longitudinally elongated fibers is visible in some regions, in others it is very much disrupted during circumferential growth of the fruit, and in sections taken below the germination valve a zone of tangentially elongated fibers lies just external to the inner epidermal layer. The fibers beyond this zone are not chaotic to the degree found in *N. sylvatica*. On the ventral side, longitudinal fibers predominate, and the dorsal wall is composed primarily of transverse fibers, many of them markedly radial in orientation. Corresponding fibers of the lateral walls are mostly oblique, as the transition is made from the radial trend to the longitudinal trend.

VASCULAR PATTERN. The flowers of *Nyssa javanica* are densely covered with hairs below the hypanthial margin, and it is necessary to remove this outer covering before the vascular system can be seen in cleared specimens. The arrangement of the bundles is very similar to that found in bilocular

¹⁴ Kirchheimer's statement (1957, p. 571) that the stones of "*Nyssa megacarpa*" are up to 40 mm. long and 20 mm. broad seems exaggerated; an illustration (p. 677, fig. 13) to which Kirchheimer refers is a photograph of an endocarp — supposedly shown about natural size — roughly 30 mm. long. Parker himself (1929) described these endocarps as 25 mm. long and 15 mm. broad.

flowers of *N. sinensis*, except that there is only one ovule and consequently only one set of ovular traces. Dorsal carpellary bundles for two carpels are present, the dorsal bundle of the missing carpel occurring on the placental side of the ovary. This "minor" dorsal is fused with a perianth bundle almost to the top of the hypanthium; whereas, the major dorsal — the one that will overlie the germination valve — is fused with a perianth bundle for only part of its length. The major ventrals are commonly fused for part or most of their length with the ventrals of the missing carpel, the combined ventrals in turn being fused with a perianth bundle. As in the *N. sylvatica* complex, adjacent ventrals occasionally are not united, in this case they may be fused with separate perianth bundles. They may also remain free to the base of the ovary. The ovule receives several strong strands from various bundles on the placental (missing carpel) side; these combine and then break up into a multitude of strands as they pass around the base of the ovule, rising high in the integument on the dorsal side.

The calyx lobes of *Nyssa javanica* are more developed than those of *N. sylvatica*, and they contain a broad vascular supply of short branches in contrast to a very vestigial supply in the latter species. The outermost lateral strands of one calyx lobe closely approximate those of adjacent lobes so that there is almost a complete circle of strands around the hypanthium apex.

The most interesting feature of the vascular system is its relationship with the dorsal ridges on the outer surface of the endocarp. Since the development of endocarp fibers does not extend into the outer layers of carpellary tissues, the position of the bundles at the carpel boundary does not influence the form of the stone in the same way as in *Nyssa sylvatica*. In fruits of the *N. sylvatica* complex the peripheral bundles and associated longitudinal fibers are sunken in grooves on the surface of the stone and the intervening areas stand out as ridges. On the other hand, a comparison of the *N. javanica* vascular pattern and the sculpturing of the stone shows that the external ridges in this species arise in the same radii as the dorsal bundle and its two flanking bundles.

Quite commonly there are a few bundles imbedded in grooves on the ventral or lateral surfaces of the *Nyssa javanica* stone, bundles which enter the ventral wall near the placenta (PL. II, FIG. 10) or run along the sides to the styler remnant. The variability in occurrence and location of such strands indicates that they are ovular and ventral bundles that have remained free of the perianth supply for all or most of their length; thus, they have been able to pass through the outer carpellary tissues and into the endocarp.

Fruit of *Nyssa aquatica*

The purple oblong to obovoid drupes of *Nyssa aquatica* are roughly 25–30 mm. long, about half as wide, and crowned by the flattened disk, the center of which is shallowly depressed. Frequently there is a marked constriction of the hypanthium just beneath the disk. Three to five long (5 to

10 mm.) hairy bracts subtend the hypanthium in very young specimens, but these fall away during fruit maturation.

Stones of this species are unilocular, obovate in outline, mucronate at the apex, and somewhat flattened (PL. I, FIGS. 1, 8). Each bears about 8 to 10 longitudinal ridges, which are very sharp and ragged-looking on the dorsal side, less so on the ventral. The major vascular bundles pass along the crests of these ridges; they are not so intimately connected with the endocarp as is the case in *Nyssa sylvatica*, and many of them are removed when the stone is cleaned. The region of the germination valve is depressed, and the flaring ventral margins of the valve are very much extended past the dorsal margins, indicating a much greater ventral than dorsal growth in the apical portion of the endocarp. The flaring ventral margins and a sharp apical point combine to give the valve of *N. aquatica* a distinctive appearance. When the fruit is boiled this distinctive appearance is enhanced because the dehiscence tissue frequently disintegrates leaving the stone agape. The endocarp wall, exclusive of the valve, is usually about 1200 μ thick in the depressed areas between the ridges; the valves are 700–900 μ thick.

The flesh was removed from more than a hundred fruits collected in Florida, South Carolina, and Georgia in order to estimate the variability in size of the endocarps. The largest of these was 28.3 mm. long, 11.2 mm. broad, and 6.5 mm. thick; the smallest, 14.8 mm. long, 9.4 mm. broad, and 4.9 mm. thick; median length, 21 mm. The length of the largest fruit is somewhat exaggerated, because it includes the woody apical "beak"; few stones are more than 26 mm. long when this projection is broken off.

HISTOLOGICAL OBSERVATIONS. The endocarp of *Nyssa aquatica* has a single inner epidermal layer of longitudinal fibers and an adjacent zone made up predominantly of tangential fibers, as in other *Nyssa* species (PL. V, FIG. 24). Elements external to the tangential zone are very disorderly, except where they extend radially toward the peripheral vascular bundles, thus forming the ridges on the surface of the stone. The sharp ridges on the endocarp of *N. aquatica*, like the less conspicuous dorsal ridges in *N. javanica*, arise in radial alignment with peripheral vascular bundles. *Nyssa aquatica* also resembles the Asiatic species because the outermost layers of carpellary tissue remain parenchymatous and do not take part in the formation of the woody endocarp. The latter similarity is best observed by comparing sections of young ovaries.

Transverse sections through the apical end of the fruit show the dehiscence tissue to be more plentiful here than in other species; no doubt this is related to the expansion of the ventral valve margins. It would be necessary for the dehiscence tissue to increase, to separate, or to elongate in order to accommodate the ventral expansion, and there is no indication that either separation or inordinate elongation has taken place. Sections through fruits that have been picked when full-grown but not completely ripe demonstrate the manner in which the dehiscence tissue matures: at this stage the endocarp is lignified almost throughout, except that the dehis-

cence tissue is still primarily parenchymatous; however, here and there isolated parenchyma cells have differentiated into very small sclereids. When the fruit is ripe, the dehiscence tissue will consist entirely of these sclereids, loosely aggregated and offering little resistance to the opening of the valve.

VASCULAR PATTERNS. In the mature fruit the positions of the dorsal and its two flanking bundles are very well marked by three prominent ridges. The flanking ridges usually connect with the basal termini of the line of dehiscence where they disappear; the dorsal ridge continues up the center of the valve. Cleared flowers show a vascular pattern similar to that of *Nyssa sylvatica* and *N. javanica*: a dorsal and two ventrals are usually fused to varying degrees with peripheral bundles that alternately supply four to seven corolla lobes and a lesser number of stamens. Corolla lobes in *N. aquatica* are the largest in the genus, and accordingly, they contain a more elaborately branched vascular supply. Occasional lobes have been found with a double vascular system, supplied by two heavy strands from the base of the ovary. There are 7 to 10 peripheral bundles arranged in a circle. In addition, when the dorsal or one of the ventral carpellaries is not fused with a peripheral bundle, it lies inside of this circle. The base of the solitary style receives, in addition to the usual three carpellary bundles, an extra strand or two from peripheral bundles on the placental side. These are, presumably, remnants of a lost carpel. Within the style the carpellary bundles ramify, forming numerous parallel strands. The ovular supply is similar to that of other *Nyssa* species in that most strands connect the placenta with peripheral bundles, but at least one independent ovular trace from the base is of common occurrence.

Fruit of *Nyssa ogeche*

The drupes of *Nyssa ogeche* are 20–35 mm. long, and, when not yet ripe, they somewhat resemble the fruits of *N. aquatica*. The disk, however, is usually more prominent and tends to retain the conical shape. Moreover, the fruit of *N. ogeche* is generally plumper, and corky spots are not so conspicuous. Ripe fruits are readily distinguished by their red color. The dense tomentum that covers the hypanthium is lost during development of the fruit except in the region immediately below the disk. Calyx lobes are not apparent, even in young material. The hairy, pointed basal bracts — usually three in number and much shorter than those of *N. aquatica* — abscise before maturity.

Stones of this species are very distinctive in appearance. They have about a dozen ridges, some of them very sharp, running longitudinally over the surface, with their crests extended radially as wide papery wings (PL. II, FIGS. 12, 13); 10–15 thick vascular strands lie in the grooves between these ridges. When the wings are removed the endocarp is seen to be quite narrow in comparison to that of other *Nyssa* species (PL. I, FIG. 2). Usually both ends are tapered and the apex is attenuated to a sharp point;

occasionally the upper end is broader and the stone oblanceolate in outline. A pronounced ventral convexity and dorsal concavity give the longer stones a boat-shaped appearance when viewed from the side; shorter stones are flattened on the dorsal side. The dorsal mid-line is marked by a groove — sometimes very deep and wide — instead of a ridge as in *N. aquatica*. The valve is acute, rather than acuminate, at the apex. It lacks the flaring ventral margins found in *N. aquatica*, but the most conspicuous ridges frequently occur near these margins, probably as a result of greater growth on the ventral side than on the dorsal. In some specimens there is a slight constriction at the base of the valve, and the stone then seems to bulge a bit above and below the constriction. Most endocarps inclose one locule, but one or two bilocular fruits can be found in every hundred. These are somewhat square in cross section, due to dorsal flattening on two faces. The wall is 600–1000 μ thick between the ridges, except along the center of the valve, where it may be 400 μ or less in thickness.

Endocarps of *Nyssa ogeche* vary considerably in their dimensions. (See PL. I, FIG. 2.) The longest encountered during this investigation measures 29.3 mm.; the shortest, 14.7 mm.; median length 23 mm. Specimens can be found as broad as 9.5 mm. and as narrow as 4.7 mm.; as thick as 7.5 mm. (bilocular) and as thin as 3.2 mm.

HISTOLOGICAL OBSERVATIONS. Except for its papery wings, the fruit of *Nyssa ogeche* resembles other *Nyssa* fruits, particularly those of the *N. sylvatica* complex, in histological composition. The endocarp has a distinct inner layer of epidermal fibers surrounded by a zone of tangential fibers. In the basal part of the fruit, tangential fibers predominate throughout the endocarp wall; higher up, the tangential zone is surrounded by a zone of fibers in which no order is distinguishable except for the radiation of the elements into the ridges. There seems to be some tendency for the outermost fibers to lie transversely and in conformity with the surface of the stone, but this tendency can be observed only in places where the ridges are not so sharp. The narrow transition region of slightly thickened cells resembles the adnation zone of *N. sylvatica*, except that the cells are larger (up to 200 μ long and 20 μ wide). Since the peripheral bundles are included within the transition, it follows that the succulent tissues are completely noncarpellary in *N. ogeche*, as in *N. sylvatica*. This transitional zone of adnation is histologically continuous with the somewhat longer, but otherwise similar, cells of the papery wings which extend radially from the ridges to the skin. The wings are three to eight cells in thickness. Morphologically they are not really a part of the endocarp; sections of flowers show that they are derived from cells of the succulent zone.

VASCULAR PATTERN. Since the corolla and the androecium are less reduced in *Nyssa ogeche* than in other *Nyssa* species, bundles supplying these parts are more numerous, and the vascular system is consequently the most complex in the genus. Five to ten short, rounded corolla lobes and seven to ten stamens (some of them imperfectly developed) are supplied

by the peripheral ring of bundles. Within this ring there is a considerable cohesion and fusion of adjacent strands. It is notable that a few branches from each staminal bundle leave the main strand and enter the conical disk, demonstrating the androecial origin of that structure. Carpellary bundles are ordinarily fused with peripheral bundles for at least half the length of the hypanthium. The dorsal carpellary bundle is easily recognizable by its prominence and by its central position in the base of the style, but the style receives so many other strands (one from almost every peripheral bundle) that the identification of two ventrals usually is not possible. Even in bilocular flowers, the two styles each receive more than three carpellaries, and the bundles ramify into several anastomosing strands after entering. Styles of unilocular flowers are superficially simple, but the rudiment of a second style can be found on close inspection. Ovular bundles seem to be more plentiful in this species than elsewhere in the genus, in keeping with the greater number of peripheral bundles with which they connect. In some cases, branches from the ovular supply pass the placenta and end blindly above it in the apical part of the endocarp, perhaps indicating the position of a lost ovule.

A closer association of the three most dorsally situated peripheral bundles is not usually noticeable in the flower and fruit of *Nyssa ogeche*; instead, all of the bundles lie fairly close together around the periphery of the narrow endocarp.

Fruit of *Camptotheca*

The outer tissues of the mature *Camptotheca* fruit are not succulent, but are dry, withered, folded, and flattened; the flattening — undoubtedly related to the development of so many fruits in a single head — usually occurs parallel to the dorsal-ventral mid-plane, giving the fruit a somewhat samaroid appearance. The surface is brown and lustrous in herbarium specimens — according to Wilson (1914), this is the natural condition — and sparsely provided with corky dots. The length is from 18–25 mm.; breadth across the widest part of the flattened outer tissues, about 7 mm.; and thickness at right angles to the flattening, only 2 or 3 mm. The outline is oblong to oblanceolate. A pulvinate disk is present at the truncated apex, around which can be seen the edge of the hypanthium with a few indistinct calyx lobes. The styler remnant is sunken in a deep pit at the center of the disk.

The narrow, thin-walled endocarp of *Camptotheca* is 15–20 mm. long and has a maximum diameter of about 2 mm. (PL. I, FIG. 6). The apex is tapered to a sharp point, and the base gradually attenuate to an even sharper point. Dorsal flattening or concavity may be evident or may be obscured by lateral compression of the fruit during development; frequently the combined effects of dorsal and lateral flattening give the upper part of the endocarp and its single locule a triangular shape in cross section. One broadly rounded ridge is present on the ventral surface of the apical third of the endocarp, and a thick, compound vascular strand can usually

be found on each side of this ridge, extending from the base of the endocarp to the placental region, and there passing into the wall. The dorsal side sometimes bears a very slight median longitudinal indentation near the apex; otherwise the endocarp is quite smooth.

Kirchheimer (1938, p. 4) erroneously reported that *Camptotheca* has no germination valve. The valve is similar in form and position to that of *Nyssa*, and it frequently opens when the fruit is boiled.

HISTOLOGICAL OBSERVATIONS. The fruit wall consists of three major zones: an outer skin of small thick-walled cells; an inner fibrous endocarp; and an intermediate zone of large thinner-walled cells, corresponding to the succulent zone of *Nyssa*. Here, however, the cells of the intermediate zone are not so thin-walled as in *Nyssa*, and they are crushed and deformed at maturity. Stone cells seem to be scattered throughout this tissue, and the peripheral bundles — quite conspicuous in *Camptotheca* fruits because of the multitude of fibers in each strand — are contained within it. The endocarp is made up of woody fibers, but these elements are much narrower (mostly under 10 μ in diameter, 400–700 μ in length) than *Nyssa* fibers. At some distance below the valve the endocarp elements are all elongated around the locule. At higher levels the outermost fibers on the ventral side are longitudinal, especially in the ventral ridge, where all of the cells are so oriented. An inner epidermis of longitudinal fibers seems to be absent. The elements are much more variable in diameter in the ridge than elsewhere; many measure 20 μ or more. The *Camptotheca* endocarp is the thinnest in the family: below the valve, it consists of about 10 fiber layers and one or two layers of transition cells, the total thickness being no more than 75 μ ; through the valve, the wall is only five or six fibers (less than 50 μ) in thickness; when measured across the ventral ridge, however, the thickness may exceed 500 μ . Along the line of dehiscence, the wall is so thin and the cells so weakly lignified that a completely transparent zone surrounds the valve in cleared whole fruits. It appears that the cells of the dehiscence tissue do not develop into sclereids; during germination the wall simply tears in this very weak region. Cleared fruits also show the orientation of fibers when viewed under the dissecting microscope: elements bordering the dehiscence tissue on the ventral side are oblique, and those within the valve are tangential. Cleared preparations further reveal that the mature endocarp is separated from the ring of peripheral bundles by a zone of transparent (thin-walled) cells; thus, it is evident that the endocarp of *Camptotheca* includes only inner carpellary tissues.

VASCULAR PATTERN. There are regularly 10 peripheral bundles in the flower; these supply the rather constantly pentamerous floral appendages (5 minute calyx lobes, 5 hairy corolla lobes, and 10 stamens in two whorls). Lateral branches in adjacent calyx lobes are usually united, forming an almost uninterrupted vascular circle around the orifice of the hypanthium. The gynoeceal vascular system is quite clearly that of three united carpels: a conspicuous major dorsal carpellary bundle is fused with a peripheral

bundle for about half the length of the hypanthium, and two lesser dorsals (belonging to lost carpels) depart from other peripherals at a higher level. Each dorsal passes into the apex of the ovary and continues as the median strand of one of the three styles. Two or three thick ventrals, apparently consisting of several thinner strands, are more centrally situated (completely within the carpellary tissues) and are not united with peripheral bundles. These rise from the base of the ovary, provide ovular branches to the placenta, and divide again as they enter the united stylar branches, thereby providing each style with two ventral strands. Since the united proximal parts of the styles are set in an invagination of the disk, the ventrals turn downward slightly before entering.

The ovule of *Camptotheca*, like that of *Nyssa*, can receive independent traces from the base of the ovary as well as strands from the ventrals; however, the ovular traces are not so plentiful here as in *Nyssa*.

Fruit of *Davidia*

Ripe fruits of *Davidia* are 28–40 mm. long, 20–30 mm. in diameter, green in color, and crowned by a pointed woody remnant of the styles. The surface may be marked with an abundance of conspicuous corky spots or with a corky reticulate pattern. It has been suggested that the two types of epidermal marking might have taxonomic significance (Li, 1954); however, the present author has seen both patterns on the same herbarium specimen. Endocarps are of the same shape as the fruit (PL. I, FIG. 9). The longest encountered during this investigation was 39 mm. in length and 17 mm. in diameter; the shortest, 25 mm. in length and 11 mm. in diameter; broader stones of intermediate length, with diameters up to 26 mm., are common. Locules number six to eight in the author's material, seven being the most frequent number. Li (1954) and others have reported that nine-locular fruits also occur. Some of the ovules in every ovary fail to develop. The abortive locules become compressed and distorted during growth, but the endocarp retains its external symmetry (PL. IV, FIG. 19). The position of each interocular septum is marked on the surface of the stone by a very thick and conspicuous longitudinal ridge, and another ridge, not quite so thick, is present along the mid-line of the long, narrow germination valve and continues to the base of the stone. This median dorsal ridge is separated from the adjacent interocular ridges by deep grooves. Countless minor grooves, longitudinal or somewhat oblique in their orientation, occur on all of the thick ridges, marking the location of small branches departing from the major vascular bundles.

Narrow germination valves, extending about two-thirds the length of the stone, are present for all locules, both fertile and abortive. These are quite thick — up to four mm., if the median dorsal ridge is included in the measurement. The septa are 700–1000 μ in thickness.

HISTOLOGICAL OBSERVATIONS. The exceedingly hard endocarp of *Davidia* is composed of sclerified elements of very variable size and wall-thickness.

In the immediate vicinity of fertile locules they are fibrous in appearance, up to 350 μ long, and up to 40 μ in diameter. In more peripheral regions they are much shorter and some cells are isodiametric. Elements with large lumina are intermixed with others having small lumina; most lumina are much larger than those of *Nyssa* fibers. An inner epidermis of longitudinal fibers is very evident in abortive locules, where circumferential growth has not taken place to such an extent as to disrupt this layer. Around each fertile locule there is a zone of more or less fibrous elements elongated circumlocularly. The septa are made up of these circumlocular elements, except where longitudinally or obliquely oriented sclereids accompany ovular traces to the placenta. Elements in the central axis of the fruit have a jumbled appearance, but they lie mostly with their long axes in the transverse plane. The peripheral cells of the stone, including those of the germination valve, seem to have no predominant orientation. The valve is outlined by a dehiscence tissue six to eight cells thick, in which smaller, rather thin-walled elements about 70 μ long and 15 μ wide are radially oriented. The *Davidia* endocarp has no outer transition zone; the woody tissue ends abruptly at the inner margin of the zone of parenchyma and stone cells that lies just beneath the leathery skin of the fruit.

Removal of the thick valves in *Davidia* is apparently facilitated by radial growth of septa during development of the endocarp. This septal expansion is sufficient to cause a folding in of the valve region, and in places the epidermis lining the valve comes to lie against that lining the septum. The line along which this double epidermis is present is radially continuous with the dehiscence tissue, and it is probable that little resistance is encountered here when germination occurs.

VASCULAR PATTERN. The vascular system of the hermaphrodite flower of *Davidia* was investigated in detail by Horne (1909), who followed the course of the bundles by means of serial cross sections. Sections and cleared specimens examined by the present author showed the same pattern reported by Horne: a peripheral ring of bundles — about three times as many as the locules — an inner ring of carpellary bundles, and two sets of about 8 to 10 ovular traces passing through each septum to adjacent placentae (PL. III, FIG. 17). The peripheral bundles supply only stamens as the epigynous calyx and corolla apparently are absent in the *Davidia* flower. The ring of carpellary bundles contains both dorsals and ventrals, all about the same distance from the axis. Ventral bundles belonging to adjacent carpels are in pairs, each pair being radially aligned with a septum. It is because of the radial elongation of cells within the septa that these bundles come to lie in the same circle with the dorsals. In the mature fruit the paired ventrals run along the crests of the septal ridges of the endocarp, and each dorsal bundle is situated on a median dorsal ridge. Some fusion of the paired ventrals is quite common. Fusion between carpellary bundles and peripheral bundles occurs to a much less extent in *Davidia*, however, than anywhere else in the Nyssaceae; when such fusion does occur, it is limited to the basal part of the flower. A pair of flanking

bundles accompanies each dorsal, but these are not to be considered homologous with the flanking bundles that appear on the dorsal side of many *Nyssa* endocarps. In *Davidia* the flanking bundles are entirely a part of the carpellary supply; whereas, in *Nyssa*, they are peripheral bundles supplying epigynous floral appendages. In the mature *Davidia* endocarp, the flanking bundles lie within the deep grooves that separate each median dorsal ridge from adjacent septal ridges. *Davidia* differs from other Nyssaceae in this respect, but a similar vascular arrangement probably prevailed in *Langtonia bisulcata*, an Eocene fruit of cornaceous affinities in which a pair of deep grooves flank the median dorsal line of each carpel (Reid and Chandler, 1933, p. 453–455). It is interesting that Horne made no mention of the flanking bundles, although he described the positions of other carpellary strands in detail; possibly the *Davidia* flowers examined by Horne were younger than those examined by the present author and some of the bundles had not yet become differentiated.

There are more traces supplying each ovule in *Davidia* than in any other member of the family. It is difficult to follow the course of these strands because they are so numerous and tend to anastomose to some extent within the septa. However, it is evident that most of the ovular traces depart from the ventral carpellary bundles in the lower part of the ovary.

Fruit of *Mastixia*

Only a relatively few fruiting specimens of *Mastixia* were examined during this investigation; therefore, the following description will draw heavily upon the detailed observations of Kirchheimer (1936), who had much more material at his disposal. According to Kirchheimer, the ovoid *Mastixia* fruit is from 20–37 mm. in length, the surface is sometimes spotted, and the apical disk may be prominent or indistinct. Throughout the genus the fruits are quite similar in appearance, and at present there is no sure way of identifying a particular *Mastixia* species by its fruit alone. Endocarps are smooth, finely creased, or knobby, and they are readily recognizable by the presence of a median dorsal furrow running from base to apex. All of the modern members of the genus seem to bear only unilocular fruits, with a solitary anatropous seed attached near the apex, as in *Nyssa*. The endocarp wall may be less than 1 mm. or more than 2.5 mm. thick, depending on the species. When the stone is cut open it can be seen that the external furrow is due to a deep longitudinal folding of the endocarp wall on the dorsal side (PL. III, FIG. 18). The fold extends inward, well past the center of the fruit, causing the locule to be horseshoe-shaped in cross section. The folding undoubtedly occurs during circumferential growth of the endocarp tissue: the author has sectioned several *Mastixia* flowers and found no furrow in this younger material.

Germination in *Mastixia* differs notably from that in *Nyssa* in that the valve separates along two lines (usually visible as thickened places in the endocarp wall) running the entire length of the stone. When the stone has

opened in this manner, the dorsal fold can be seen as a narrow, but very prominent, median ridge on the internal surface of the valve.

HISTOLOGICAL OBSERVATIONS. The fruit wall consists of three major tissue zones: a leathery outer skin, an inner sclerified endocarp, and an intermediate zone in which parenchyma and stone cells are intermixed. Stone cells are extremely abundant, and they seem to mature much earlier than the woody cells of the endocarp. One fruit examined by the author, *J. & M. S. Clemens 30477 (A)*, from Borneo, and identified by Danser as *Mastixia trichotoma* Blume (although E. D. Merrill considered it an undescribed species), had the external appearance and the hardness of a mature fruit, but inspection of transverse sections revealed that the endocarp was still thin-walled and incompletely developed and that the hardness of the fruit wall was due to the predominance of fully developed stone cells in the outer tissues. It is interesting in this connection that *Mastixia* fruits generally show no external mark of the dorsal endocarpic fold: probably it is the rigidity imparted by the stone cells that prevents outer tissues from being folded inward along with the endocarp.

Numerous secretory canals are present in the material studied by the author. These run longitudinally through the same tissue zone in which stone cells are so abundant. Usually — perhaps always — they are associated with vascular bundles, and sections of flowers show that they accompany some of the bundles into the calyx lobes. According to Kirchheimer (1936), the canals are fewer in number in some species and altogether absent in others.

Kirchheimer reported that the *Mastixia* endocarp consists of three recognizable tissue zones: one to five layers of thick-walled and more or less isodiametric cells at the periphery of the stone, a central zone of radially elongated sclereids, and a wider inner zone of fibers surrounding the locule. A sectioned endocarp of *M. arborea* Clarke (Burma, *J. H. Lace 5641, A*) shows these zones very well (PL. V, FIG. 22). The isodiametric cells are mostly confined to a single outer layer, a layer that could possibly be interpreted as the outer epidermis of the carpellary tissues. The radially elongated elements (about 120 μ long and 50 μ in diameter) are arranged in a few roughly concentric layers around the inner zone of fibers. The latter elements are longer (up to 250 μ) and more slender than the radial elements; most of them are elongated concentrically, but groups of longitudinal elements occur in places. Both transverse and longitudinal elements are present in the outer part of the dorsal fold, but the innermost extension of the fold is made up exclusively of longitudinal elements. An inner epidermal layer of longitudinal cells is apparently lacking in *Mastixia*; it is possible, however, that such a layer is formed at an earlier stage of development and is later disrupted by the very great circumferential growth of the endocarp tissue. Most cells in the endocarp have thinner walls and larger lumina than the fibers of a *Nyssa* stone. Another endocarp examined by the author, believed to belong to *M. philippinensis* Wangerin (collection data lost) is made up of cells with even thinner walls, and the zone of

radially elongated cells is not well defined. Kirchheimer also observed that *M. philippinensis* lacks a distinct zone of radial elements.

Kirchheimer noted that dehiscence takes place along two lines that show up in transverse sections as thickened places in the endocarp wall and that the opening of the valve is associated with the disintegration of parenchyma cells in these thicker places. He failed to note that the thick places always occur precisely where two important vascular bundles rise from the base of the endocarp to the placenta. The bundles are surrounded by a large number of very thick-walled longitudinal fibers, and the presence of these elements probably facilitates longitudinal splitting of the valve along the path of the inclosed vascular strand (PL. V, FIG. 21).

It should be clear that the dehiscence mechanism of *Mastixia* differs substantially from that of all Nyssaceae. In the latter group the vascular bundles — especially the ovular traces — determine the position of the dehiscence tissue only indirectly, by their effect on the orientation of neighboring endocarp fibers; there are no vascular strands actually within the dehiscence tissue. In *Mastixia*, on the other hand, the endocarp splits exactly where two ovular traces pass through the endocarp from base to placenta. The line of dehiscence is independent of the ovular supply only for a very short distance between the placenta and the apex of the stone. An inspection of sections taken above the placenta suggests that orientation of the cells plays a part in the dehiscence of the valve in this limited apical region, where there are no bundles in the endocarp save the dorsal carpellary bundle.

VASCULAR PATTERN. Several flowers from two species of *Mastixia*, *M. philippinensis* (Luzon, Ramos 23353, GH) and *M. trichotoma* var. *maingayi* Clarke (Sumatra, Neth. Ind. For. Serv. 98 T.3P.261, A), were cleared, and some were subsequently sectioned, but in neither case could the vascular pattern be established very satisfactorily. The flowers are tiny and coated with lignified hairs, and the inner tissues are filled with a persistent dark substance, perhaps resulting from the presence of the secretory canals. Moreover, the bundles and associated canals are very numerous, making it difficult to follow the path of any one of them in the rather distorted tissues of flowers taken from herbarium specimens. Serial sections of the fruits proved to be more useful in this respect, but vascularization of the floral appendages and of the style is still imperfectly understood.

It is quite evident, however, that the vascular pattern of *Mastixia* flowers and fruits differs in two important respects from that found in *Nyssa*, *Camptotheca*, or *Davidia*: (1) the numerous bundles passing through the zone of parenchyma and stone cells to the calyx lobes and other epigynous parts are not in a single circle, but are spirally arranged, a pattern that can best be seen in sections taken near the base or near the apex; (2) there are only three vascular strands, the dorsal carpellary bundle and two ovular traces, within the endocarp tissue. Although it was not possible with the material at hand to trace most of the spirally arranged outer bundles into their respective appendages, it appears that each of the well developed

calyx lobes receives more than one strand. Additional bundles presumably enter the four or five petals and the equal number of stamens. There are many more bundles, however, than there are floral parts, and it is likely that some of these proceed into the disk, which (at least in *M. trichotoma* var. *maingayi*) is not pulvinate, but is in the form of a thick collar around the style. Ventral carpellary bundles could not be identified in any of the specimens examined. It is possible that they no longer exist in the reduced gynoecium of *Mastixia*. The ovular traces are unconnected with any of the outer bundles from the base to the placenta: it may be that the two strands actually represent a complete phylogenetic fusion of ventral carpellary bundles with ovular traces; however, there is no continuation of these strands into the style to prove this point. The dorsal bundle is the most prominent bundle in the fruit; it is located within the outer part of the median dorsal fold, where the accompanying parenchyma frequently ruptures, leaving a conspicuous longitudinal hollow space. This bundle is also unconnected with any of the outer bundles.

MORPHOLOGICAL SUMMARY

It seems advisable at this point to summarize the major morphological features of the nyssaceous fruit so that the reader will better be able to follow the subsequent discussion of relationships between species.

(1) Only the inner part of the fruit wall is derived from carpellary tissues; the outer part is derived from the hypanthium, as is the case in most fruits that develop from flowers with inferior ovaries (Douglas, 1957; Eames, 1961). There is no epidermis between carpellary and extracarpellary tissues, but the boundary may be located by means of the vascular bundles. Tissues internal to the carpellary bundles are certainly carpellary tissues, and those tissues that are external to all bundles supplying the perianth must be considered a part of the hypanthium. In *Nyssa* and *Camptotheca*, bundles supplying the androecium are fused for most of their length with bundles supplying the perianth, and the fusion products are in turn fused with carpellary bundles, resulting in a single circle of compound vascular strands. These compound strands mark the transition between carpellary and extracarpellary tissues.

(2) In the *Nyssa sylvatica* complex and in *N. ogeche*, all of the carpellary tissues become woody. In *N. javanica*, *N. aquatica*, *Camptotheca*, and *Davidia*, the outermost layers of carpellary tissue remain parenchymatous. The stones of all species have a distinct inner zone of transverse fibers, elongated parallel with the locule. Taken alone, this inner zone of the nyssaceous endocarp is roughly comparable to some of the woody endocarps that develop in other plant groups, where the ovary is superior.

(3) Those species in which the entire carpellary portion of the fruit wall becomes woody produce endocarps marked by vascular bundles lying in longitudinal grooves, with the regions between the bundles protruding as ridges. Species in which the outer carpellary tissues remain parenchymatous produce smooth endocarps (*Camptotheca*) or ridged endocarps in

which the ridges are radially aligned with major vascular bundles (*Nyssa aquatica*, *Davidia*). The stone of *N. javanica* combines both of these features: it is relatively smooth, and its three inconspicuous dorsal ridges arise opposite bundles.

CONCLUSIONS

SIMILARITY OF VASCULAR PATTERNS IN NYSSA AND CORNUS. Vascular patterns in the flowers of *Nyssa* resemble very closely the vascular patterns of *Cornus* described by Wilkinson (1944). Wilkinson's generalized drawings (p. 279, figs. 1-7) representing several species of *Cornus* show a more elaborate sepallary supply than that of *Nyssa* and a somewhat different orientation of the ovule. There is a further difference in the number of peripheral bundles, for the flowers of *Cornus* are usually tetramerous and accordingly there are only eight bundles supplying the perianth. In important respects, however, the drawings are equally representative of bilocular *Nyssa* flowers; carpellary bundles are variously fused with peripheral bundles; ventrals of adjacent carpels are united for much of their length; and the ovular supply is made up of numerous traces. According to Wilkinson's descriptions, ovular traces in *Cornus* always connect with the ventrals. This is a somewhat simpler condition than that found in *Nyssa*, where ovular traces may also connect with peripheral bundles or may rise independently from the base of the ovary.

Comment is necessary regarding Wilkinson's notion that the bilocular ovary in *Cornus* has been derived from a unilocular ovary. She concluded from her study of the vascular pattern that the partition separating the two locules is not a true septum, but a pair of fused parietal placentae, citing the occurrence of an incompletely formed partition in *C. suecica* in support of her argument. Since the vascular patterns in *Cornus* and *Nyssa* are so similar, Wilkinson's conclusion, if valid, could be extended to include the nyssaceous ovary. To the present author, however, the notion that the septum in either genus is derived from fused placentae seems extreme and unjustified. Wilkinson's interpretation of the vascular system with regard to this point is not at all convincing, and her use of an unusual specimen of *C. suecica*, which she herself recognized as an advanced member of the genus, to demonstrate a supposedly primitive character is open to question. If Wilkinson's view were correct, one would expect at least some of the fossil fruits of Nyssaceae and Cornaceae to be unilocular with two or more prominent parietal placentae. Such fruits are not known. On the contrary, numerous fossil cornaceous and nyssaceous fruits dating from as long ago as the Eocene show the multilocular condition, and locules are more numerous in these ancient fruits than in their modern counterparts. Furthermore, if the septum were an advanced feature derived from the fusion of parietal placentae, one would expect unilocular fruits of modern *Cornus* to retain two placentae and two seeds. On the contrary, unilocular fruits of *Cornus* resemble those of *Nyssa* (Kirchheimer, 1948). Recently

Mittal (1960, p. 116) has also expressed disagreement with Wilkinson's concept of the septum.

AFFINITIES AMONG NYSSA SPECIES. Perhaps the most interesting result of this investigation is the discovery of a resemblance between fruits of the Asiatic *N. javanica* and the American *N. aquatica*. Since the development of the endocarp in these two species is so different from that of other *Nyssa* species, the idea that *N. javanica* and *N. aquatica* are somehow related seems very attractive. *Nyssa aquatica* is the more advanced species in several respects. The inflorescence on hermaphrodite trees has been reduced to a solitary flower, and the gynoeceium, since it shows little or no evidence of the ancestral polymeric condition, is the most reduced of all *Nyssa* species. Reduction is also evident in the number of corolla lobes and in the number and fertility of the stamens present in hermaphrodite flowers. Furthermore, data from the anatomical studies of Titman (1949) may be interpreted to indicate that the wood of *N. aquatica* is more advanced than the wood of *N. javanica*. (In *N. aquatica* the vessel members are shorter and the perforation plates have fewer scalariform bars.) If the two species are indeed related, then *N. javanica* must be much closer to the ancestral form. It will be shown in a later paper that well-preserved fossil fruits of the same general morphological type as *N. javanica* fruits have been collected in early Tertiary deposits of the eastern United States. When the fossil record is considered along with the morphological similarity of the modern fruits, the affinity of *N. javanica* and *N. aquatica* can scarcely be doubted.

Affinities within the *Nyssa sylvatica* complex are sufficiently evident that little discussion is necessary. The same features that separate *N. sinensis* from its American counterparts, notably the pedicellate bisexual inflorescence and the frequent occurrence of bilocular fruits, mark the Chinese species as the most primitive member of the complex. It seems likely that the greater abundance of trichomes on young leaves and inflorescences of *N. sinensis* is also a primitive characteristic. (In this connection it may be noted that the flowers of the advanced species *N. aquatica* are glabrous; whereas those of *N. javanica* are hairy.)

Since *Nyssa biflora*, somewhat hesitantly treated in this paper as a separate species from *N. sylvatica*, has a more reduced inflorescence than the latter, it must be assumed that *N. sylvatica* is the older of these two.

The *Nyssa sylvatica* complex seems not to bear a very close relationship to *N. javanica* and *N. aquatica*. The fruits of the two latter species are histologically different from those of the *N. sylvatica* complex, and there are accompanying floral differences: staminate flowers are borne in capitate inflorescences in *N. javanica* and *N. aquatica*; in short racemes in the *N. sylvatica* complex. To the morphological differences may be added the recent report of Johnson and Fairbrothers (1961) that *N. sylvatica* and *N. aquatica* can be distinguished by serological methods. These facts indicate that the *N. sylvatica* complex has evolved independently of *N. javanica*

and *N. aquatica* for quite a long time. Fossil evidence will be adduced to support this view.

The question may arise as to which of the two evolutionary lines retained more of the remote ancestral features. Actually both lines appear to have advanced as well as primitive characteristics. The short racemose inflorescences and frequent bilocular gynoecia of *Nyssa sinensis* show less evidence of reduction than the capitate inflorescences and unilocular gynoecia of *N. javanica*. On the other hand, a stone formed only from inner cell layers of the carpel is probably more primitive than a stone formed from an entire gynoecium. In this respect *N. javanica* and *N. aquatica* retain the more primitive structure.

Thus far *Nyssa ogeche* has not been mentioned in this discussion because that species shows no very close affinity with any other in the genus. Except for the dense covering of trichomes, the capitate staminate inflorescence and solitary hermaphrodite flower of *N. ogeche* resemble corresponding structures of *N. aquatica*. Moreover, Titman (1949) found that the wood of *N. ogeche*, like that of *N. aquatica*, is a bit more advanced in some ways than the wood of other *Nyssa* species.¹⁵ On these grounds, Titman suggested that *N. ogeche* has been derived from *N. aquatica*. Titman's suggestion must now be rejected emphatically because the flowers of *N. ogeche*, with their double styles and their more numerous stamens and corolla lobes, cannot have been derived from the reduced flowers of *N. aquatica*. If there were a close relationship between these two species, it would perforce be in the other direction, with *N. ogeche* being the more primitive. However, the structure of the endocarp of *N. ogeche* is not at all like that of *N. aquatica*; rather, it resembles both externally and internally the endocarp found in the *N. sylvatica* complex. In fact, when the papery wings have been removed from some of the shorter stones of *N. ogeche*, these could be mistaken for elongated stones of *N. sylvatica* or *N. biflora* (PL. I, FIG. 7). It seems most likely that this puzzling species is not intimately related to any other modern *Nyssa* and that it has had a long evolutionary history of its own.

RELATIONSHIP OF CAMPTOTHECA AND NYSSA. The observations reported in this paper support the opinion of other workers that *Nyssa* and *Camptotheca* are closely allied. Titman (1949), noting that the vessel members in *Camptotheca* are more advanced in some respects than those of *Nyssa*, suggested that *Camptotheca* has been derived from the ancestors of *N. javanica*. Considering the structure of the fruits and the inflorescences of the two plants, this is a reasonable deduction. In *Camptotheca* the outer cell layers of the carpellary portion of the fruit wall remain parenchymatous, indicating a relationship with *N. javanica*. Moreover, *Camptotheca*

¹⁵ Users of Titman's data are cautioned that there are errors in the ratios of length to width employed to evaluate the degree of specialization of vessel members. For instance, the average length of vessel members in wood of *Nyssa ogeche* was reported as 802 μ , the average width as 49 μ , and the ratio as 10:1 (see both text and table on p. 254 of Titman's paper). Assuming measurements are accurate, the correct ratio is 16:1, of course.

is more specialized than the latter species with regard to dispersal of its fruits. The reduced vascular pattern, the dry outer fruit wall, the thin, light endocarp, and the great abundance of fruits in each head are correlated aspects of this specialization. Presumably the fruits of the ancestral plants resembled much more those of modern *N. javanica* than those of *Camptotheca*. The gynoecium must have been at least trimerous (but not necessarily trilocular), however, since three styles are still present in *Camptotheca*. Probably in this ancestral population, as in modern *Camptotheca*, there were not two kinds of sexually different trees.

PRIMITIVE AND ADVANCED FEATURES IN DAVIDIA. In most respects the hermaphrodite flowers of *Davidia* are much less advanced than those of other Nyssaceae. The gynoecium is usually heptamerous, and there are more than 20 stamens. Vascular bundles are very numerous, and fusion of peripheral strands with carpellaries is slight. Furthermore, woody elements of the endocarp in the mature fruit are not nearly so long, narrow, and thick-walled as in *Nyssa*. All of these features must have persisted since very remote times.

There are other characteristics of the reproductive structures of *Davidia* that are not primitive, however. The pedicels bearing the staminate flowers have been reduced so much as to be almost non-existent, and it is likely that the perianth has also been lost through reduction. Moreover, the occurrence of a single hermaphrodite flower on an otherwise staminate inflorescence can only be interpreted as a specialization.

Although *Davidia* has received much attention as an ornamental plant, it seems that little effort has been directed toward a morphological interpretation of the curious inflorescence. Actually there are two inflorescences present wherever the hermaphrodite flower appears — a capitate staminate inflorescence and a hermaphrodite inflorescence that has been reduced to a solitary flower. Serial sections of the staminate inflorescence show that the thick axis branches into two equal parts just below the insertion of the hermaphrodite flower. Evidently the compound inflorescence of *Davidia* has evolved by reduction from a panicle of inflorescences like that still found in *Camptotheca*. Hermaphrodite flowers of *Camptotheca* are located in the most distal inflorescences, and it appears that the hermaphrodite flower (inflorescence) of *Davidia* also occupies a position distal to the staminate inflorescence. The latter inference is based on the fact that the more distally situated of the two large, white subtending bracts is always attached on the same side of the main axis as the hermaphrodite flower. Li and Schramm (1954) report that two hermaphrodite flowers can occasionally occur on a single staminate head. It would be interesting to know whether both flowers in such cases belong morphologically to the same hermaphrodite inflorescence or whether there are two hermaphrodite inflorescences involved.

RELATIONSHIP OF MASTIXIA TO NYSSACEAE. The resemblance of the *Mastixia* fruit to fruits of Nyssaceae is considerably less than expected.

There are histological similarities, but differences in the vascular pattern and in the establishment of the dehiscence line are more impressive. Considering the marked resemblance of vascular patterns between *Nyssa* and *Cornus*, the dissimilarity encountered in *Mastixia* is surprising. One must infer that *Mastixia* is not so closely related to the Nyssaceae as are some other cornaceous genera.

An interesting assortment of primitive and advanced features are combined in *Mastixia*. The panicle of perfect flowers is about as primitive as any inflorescence in the Umbellales, and vessels in the secondary xylem are similarly primitive. If, as it seems, the numerous peripheral vascular bundles in the flower are spirally arranged, that may also be taken as a primitive feature. In contrast, the vascular supply of the gynoecium is very much reduced. In specimens examined for this study, only two bundles supply the ovule and no vestiges of lost carpels are present. Without additional information this gynoecium would be considered truly monomerous, but in view of the multilocular condition of fossil mastixioid fruits (Kirchheimer, 1936) and the recognizable pseudomonomerous nature of unilocular gynoecia in related genera, it must be concluded that the gynoecium in *Mastixia* is also pseudomonomerous.

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LITERATURE CITED

- ADAMS, J. E. 1949. Studies in the comparative anatomy of the Cornaceae. Jour. Elisha Mitchell Soc. **65**: 218-244.
- ANONYMOUS. 1942. Big trees: Maryland's black gum. Am. Forests **48**: 100.
- APPLEQUIST, M. B. 1959a. Longevity of submerged tupelogum and bald-cypress seed. La. State Univ. Forestry Notes No. 27, 2 pp.
- . 1959b. Soil-site studies of southern hardwoods *in* Southern forest soils. La. State Univ. Sch. Forestry Proc. Forestry Symposium **8**: 49-63.
- ARNOTT, H. J. 1959. Leaf clearings. Turtox News **37**: 192-194.
- BALDWIN, H. I. 1961. Succession in a black gum-red maple swamp — a twenty-five year record. N.H. Forestry and Recreation Comm. Caroline A. Fox Res. & Demon. Forest. Fox Forest Notes No. 86, 2 pp.

- BARGHOORN, E. S. 1948. Sodium chlorite as an aid in paleobotanical and anatomical study of plant tissues. *Science* **107**: 480-481.
- . 1950. The Brandon lignite. *Joint Bull. Vt. Bot. & Bird Clubs*, **18**: 21-36.
- & W. SPACKMAN, JR. 1949. A preliminary study of the flora of the Brandon lignite. *Am. Jour. Sci.* **247**: 33-39.
- BEAN, W. J. 1950. *Trees and shrubs hardy in the British Isles*. 7th ed. 3 vol. John Murray, London.
- BOR, N. L. 1938. A sketch of the vegetation of the Aka Hills, Assam: a synecological study. *Indian For. Rec.* **1**(4): 103-221.
- BRAUN, E. L. 1950. *Deciduous forests of eastern North America*. Blakiston Co., Philadelphia.
- CHU, K.-L., & W. S. COOPER. 1950. An ecological reconnaissance in the native home of *Metasequoia glyptostroboides*. *Ecology* **31**: 260-278.
- COWAN, J. M. 1929. The forests of Kalimpong. *Rec. Bot. Surv. India* **12**: 1-74.
- DANSER, B. H. 1934. The Cornaceae, *sensu stricto*, of the Netherlands Indies. *Blumea* **1**: 46-74.
- DEMAREE, D. 1932. Submerging experiments with *Taxodium*. *Ecology* **13**: 258-262.
- DERMEN, H. 1932. Cytological studies of *Cornus*. *Jour. Arnold Arb.* **13**: 410-415.
- DIXON, D. 1961. AFA's social register of big trees; these are the champs. II. *Am. Forests* **67**(2): 41-47.
- DOUGLAS, G. E. 1957. The inferior ovary. II. *Bot. Rev.* **23**: 1-46.
- EAMES, A. J. 1961. *Morphology of the angiosperms*. McGraw-Hill Co., New York.
- ERDTMAN, G. 1952. *Pollen morphology and plant taxonomy: angiosperms*. Chronica Botanica, Waltham, Mass.
- ESAU, K. 1953. *Plant anatomy*. Wiley & Sons, New York.
- EYLES, D. E. 1941. The status of *Nyssa acuminata* Small. *Castanea* **6**: 32-35.
- FERNALD, M. L. 1935. The varieties of *Nyssa sylvatica*. *Rhodora* **37**: 433-437.
- GAMBLE, J. S. 1902. *A manual of Indian timbers*. Revised ed. Sampson, Low, Harston, & Co., London.
- HALL, T. F., & W. T. Penfound. 1939. A phytosociological study of a *Nyssa biflora* consocieties in southeastern Louisiana. *Am. Midl. Nat.* **22**: 369-375.
- HARMS, H. 1898. Cornaceae in Engler & Prantl. *Nat. Pflanzenfam.* III. **8**: 250-270.
- HARPER, R. M. 1928. *Economic botany of Alabama*, part 2. *Geol. Surv. Ala. Monogr.* 9.
- HEMSLEY, W. B. 1912. *Davidia involucrata* var. *vilmoriniana*. *Bot. Mag.* 128, t. 8432.
- HORNE, A. S. 1909. The structure and affinities of *Davidia involucrata* Baill. *Trans. Linn. Soc.* II. **7**: 303-326.
- . 1914. A contribution to the study of the evolution of the flower, with special reference to the Hamamelidaceae, Caprifoliaceae, and Cornaceae. *Ibid.* **8**: 239-309.
- HU, H. H. 1927. *Nyssa sinensis*. In: Hu & Chun. *Icones Plantarum Sinicarum*. Fascicle 1. Commercial Press, Shanghai.
- HUTCHINSON, J. 1959. *The families of flowering plants*. Ed. II. Clarendon Press, Oxford.
- JOHNSON, M. A., & D. E. FAIRBROTHERS. 1961. Serological correspondence between the Cornaceae and Nyssaceae. *Abstract. Am. Jour. Bot.* **48**: 534.

- KIRCHHEIMER, F. 1936. Zur Kenntnis der Früchte rezenter und fossiler Mastixioideen. *Beih. Bot. Centralbl. Abt. B.* **55**: 275-300.
- . 1938. *Cornaceae*. *Fossilium Catalogus II: Plantae*. **23**: 1-210.
- . 1943. Die Mastixioideen in der Flora der Gegenwart. *Braunkohle*, 1943, Heft **2**: 17-19 & Heft **3**: 26-30.
- . 1948. Über die Fachverhältnisse der Früchte von *Cornus* L. und verwandter Gattungen. *Planta* **36**: 85-102.
- . 1957. Die Laubgewächse der Braunkohlenzeit. Wilhelm Knapp, Halle a.d. Saale.
- KOORDERS, S. H., & T. VALETON. 1900. *Nyssa* (Cornaceae). Bijdrage tot de Kennis der Boomsorten op Java. *Meded. Lands. Plantent.* **33**(Bijdr. 5): 95-101.
- LI, H.-L. 1952. Floristic relationship between eastern Asia and eastern North America. *Trans. Am. Phil. Soc. II.* **42**: 371-429.
- . 1954. *Davidia* as the type of a new family Davidiaceae. *Lloydia* **17**: 329-331.
- & C.-Y. CHAO. 1954. Comparative anatomy of the woods of Cornaceae and allies. *Quart. Jour. Taiwan Mus.* **7**: 119-136.
- & J. R. SCHRAMM. 1954. *Davidia* in the Philadelphia region. *Morris Arb. Bull.* **5**: 31-33.
- MCINTOSH, R. P. 1959. Presence and cover in pitch pine-oak stands of the Shawangunk Mts., New York. *Ecology* **40**: 482-485.
- MERRILL, E. D. 1937. *Miscellanea Sinensia*. *Sunyatsenia* **3**: 246-262.
- . 1938. New or noteworthy Indo-Chinese plants. *Jour. Arnold Arb.* **19**: 21-70.
- & W.-Y. CHUN. 1940. Additions to our knowledge of the Hainan flora, III. *Sunyatsenia* **5**: 1-200.
- & L. M. PERRY. 1940. *Plantae Papuanae Archboldianae*, IV. *Jour. Arnold Arb.* **21**: 511-527.
- METCALFE, C. R., & L. CHALK. 1950. *Anatomy of the dicotyledons*. 2 vols. Clarendon Press, Oxford.
- MIRANDA, F., & A. J. SHARP. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology* **31**: 313-333.
- MITTAL, S. P. 1960. Studies in the Umbellales. I. An abstract. *Agra Univ. Jour. Res. Sci.* **9**: 113-119.
- MONACHINO, J., & E. C. LEONARD. 1959. A new species of *Justicia* from Florida. *Rhodora* **61**: 183-187.
- OERTEL, E. 1934. "White tupelo" of western Florida. *Am. Bee Jour.* **74**: 310-312.
- PARKER, R. N. 1929. The Indian species of *Nyssa* Linn. *Indian Forester* **55**: 642-645.
- PENFOUND, W. T. 1952. Southern swamps and marshes. *Bot. Rev.* **18**: 413-446.
- & T. F. HALL. 1939. A phytosociological analysis of a tupelo gum forest near Huntsville, Ala. *Ecology* **20**: 358-364.
- PHILPOTT, J. 1956. Blade tissue organization of foliage leaves of some Carolina shrub-bog species as compared with their Appalachian Mountain affinities. *Bot. Gaz.* **118**: 88-105.
- POPHAM, R. A., T. J. JOHNSON, & A. P. CHAN. 1948. Safranin and anilin blue with Delafield's hematoxylin for staining cell walls in shoot apices. *Stain Technol.* **23**: 185-190.
- RAHMLow, H. J. 1960a. Tupelo honey production. *Gleanings Bee Culture* **88**: 457-461, 509.

- . 1960b. Our nation's highest-priced honey. *Ibid.* **88**: 532–534.
- REID, E. M., & M. E. J. CHANDLER. 1933. The London Clay flora. British Museum (Nat. Hist.), London.
- RICKETT, H. W. 1945. Nyssaceae. *N. Am. Fl.* **28B**: 313–316.
- RODRIGUEZ, R. L. 1957. Systematic anatomical studies on *Myrrhidendron* and other woody Umbellales. *Univ. Calif. Publ. Bot.* **29**: 145–318.
- SARGENT, C. S. 1893. Cornaceae in *The silva of North America* **5**: 73–84.
- . 1922. *Manual of the trees of North America*. Ed. 2. Houghton Mifflin Co., Boston.
- SHARP, A. J., & E. HERNANDEZ X. 1945. Distribucion de la *Nyssa sylvatica* Marsh. en Mexico. *Bol. Biol. Univ. Puebla* **12**: 13–15.
- SHUNK, I. V. 1939. Oxygen requirements for germination of *Nyssa aquatica*. *Science* **90**: 565–566.
- SMALL, J. K. 1903. *Flora of the southeastern United States*. Published by the author, New York.
- . 1927. A new *Nyssa* from Florida. *Torreyana* **27**: 92–93.
- STEWART, A. N. 1958. *Manual of vascular plants of the Lower Yangtze Valley*. Oregon State College, Corvallis.
- TITMAN, P. W. 1949. Studies in the woody anatomy of the family Nyssaceae. *Jour. Elisha Mitchell Soc.* **65**: 245–261.
- WANG, C.-W. 1961. *The forests of China*. Maria Moors Cabot Found. Publ. No. 5. Harvard Univ., Cambridge.
- WANGERIN, W. 1910. Nyssaceae in A. Engler. *Das Pflanzenreich*, IV. **220a**: 1–20.
- WASSCHER, J. 1935. The genus *Nyssa* in the Netherlands Indies. *Blumea* **1**: 344–350.
- . 1948. Nyssaceae. *Fl. Malesiana I.* **4**: 29–31.
- WELLS, B. W. 1942. Ecological problems of the southeastern United States Coastal Plain. *Bot. Rev.* **8**: 533–561.
- WETMORE, R. H. 1932. The use of celloidin in botanical technic. *Stain Technol.* **7**: 37–62.
- WILKINSON, A. M. 1944. Floral anatomy of some species of *Cornus*. *Bull. Torrey Club* **71**: 276–301.
- WILSON, E. H. 1913. *A naturalist in western China*. 2 vols. Doubleday, Page Co., New York.
- . 1914. Nyssaceae in Sargent, C. S. *Plantae Wilsonianae* **2**: 254–257.
- WODEHOUSE, R. P. 1935. *Pollen grains*. McGraw-Hill, New York.
- WOOD, L. B. 1958. White tupelo — rarest of honeys. *Fla. Grower & Rancher*, March, 1958, p. 17.

DIVISION OF WOODS,
SMITHSONIAN INSTITUTION,
WASHINGTON 25, D.C.

EXPLANATION OF PLATES

PLATE I

FIG. 1. Stones of *Nyssa aquatica* (author's collection), natural size. Specimens in upper right lateral view; others viewed from dorsal side. FIG. 2. Stones of *N. ogeche* (author's collection) with papery wings removed, showing variation in size and shape. Three specimens on right in bottom row are viewed from ventral (placental) side; others shown in dorsal or lateral view. FIG. 3. Variation in stones of the *N. sylvatica* complex; all specimens natural size and viewed from dorsal side. Top row, *N. sinensis*: (left to right) *Steward & Cheo 818* (A), "Yung Hsien, Ta Tseh Tsuen"; *R. C. Ching 3031* (A), Anhwei; *Y. Tsiang 5944* (A), "Yunfoushan, Tuyun"; *C. Wang 39489* (A), Kwangsi (two fruits). Center row, *N. biflora*: *A. Traverse 498* (GH), Ga.; *R. K. Godfrey 6433* (GH), N. C.; *Godfrey & Tryon 1462* (GH), S. C.; *W. W. Eggleston 4919* (GH), Va.; *A. E. Radford 6327* (GH), N.C. Bottom, *N. sylvatica*: *Svenson 10372a* (GH), Tenn.; *E. T. & S. A. Harper s. n.* (A), Charlestown, W. Va.; *F. MacKeever MV306* (NEBC), Mass. FIG. 4. *N. sylvatica* stone (*Svenson 10372*), $\times 2$; viewed from placental side—note two pits where ovular strands, rising independently from base, enter endocarp wall en route to placenta. FIG. 5. Lateral view of stones shown in FIG. 3: (left to right) *Steward & Cheo 818*, *MacKeever MV306*, *Traverse 498*, *E. T. & S. A. Harper s. n.*, *Godfrey 6433*. Natural size. FIG. 6. Fruits of *Camptotheca acuminata* (*A. Henry 13433*, A), from Yunnan, natural size—outer tissues have not been removed from fruit on left. FIG. 7. To show similarity between unusually long *N. biflora* stones and shortest stones of *N. ogeche*. First and third specimens from left are *N. biflora* (*A. Traverse 498*). FIG. 8. *N. aquatica* stone (author's collection), $\times 2$; viewed from ventral side. FIG. 9. *Davidia* stone (collected *E. H. Wilson*, China), $\times 2$ —note partially opened germination valve with prominent median dorsal ridge flanked by two deep grooves.

PLATE II

FIG. 10. Stone of "*Nyssa megacarpa*" (*Parker 2308*, A) between two smaller *N. javanica* stones from Sumatra (*Forbes 2880*, GH), all $\times 2.7$. Smaller stones shown in ventral (above) and dorsal view. FIG. 11. Transverse section, $\times 7$, of *N. javanica* stone, taken below the valve, showing sculpturing of locule. Dorsal side is at bottom of photo. FIG. 12. *N. ogeche* fruit, $\times 2.7$, with skin and fleshy tissue removed carefully to show papery wings radiating from stone. FIG. 13. Transverse section, $\times 7$, of *N. ogeche* stone, taken at base of valve—note position of peripheral bundles between ridges, abundance of ovular traces in endocarp wall. Dorsal carpellary bundle is prominent above number "13," and basal part of dehiscence tissue can be seen at lower left.

PLATE III

FIG. 14. Longitudinal section, $\times 23$, of *Nyssa sylvatica* flower (petals and stamens no longer attached)—note nectariferous disk above rim of hypanthium and three major tissue zones that will form the fruit wall. Note also the single vascularized integument surrounding narrow nucellar peg. FIG. 15. Transverse section, $\times 30$, of *N. sylvatica* flower (collected May 20th), showing eight

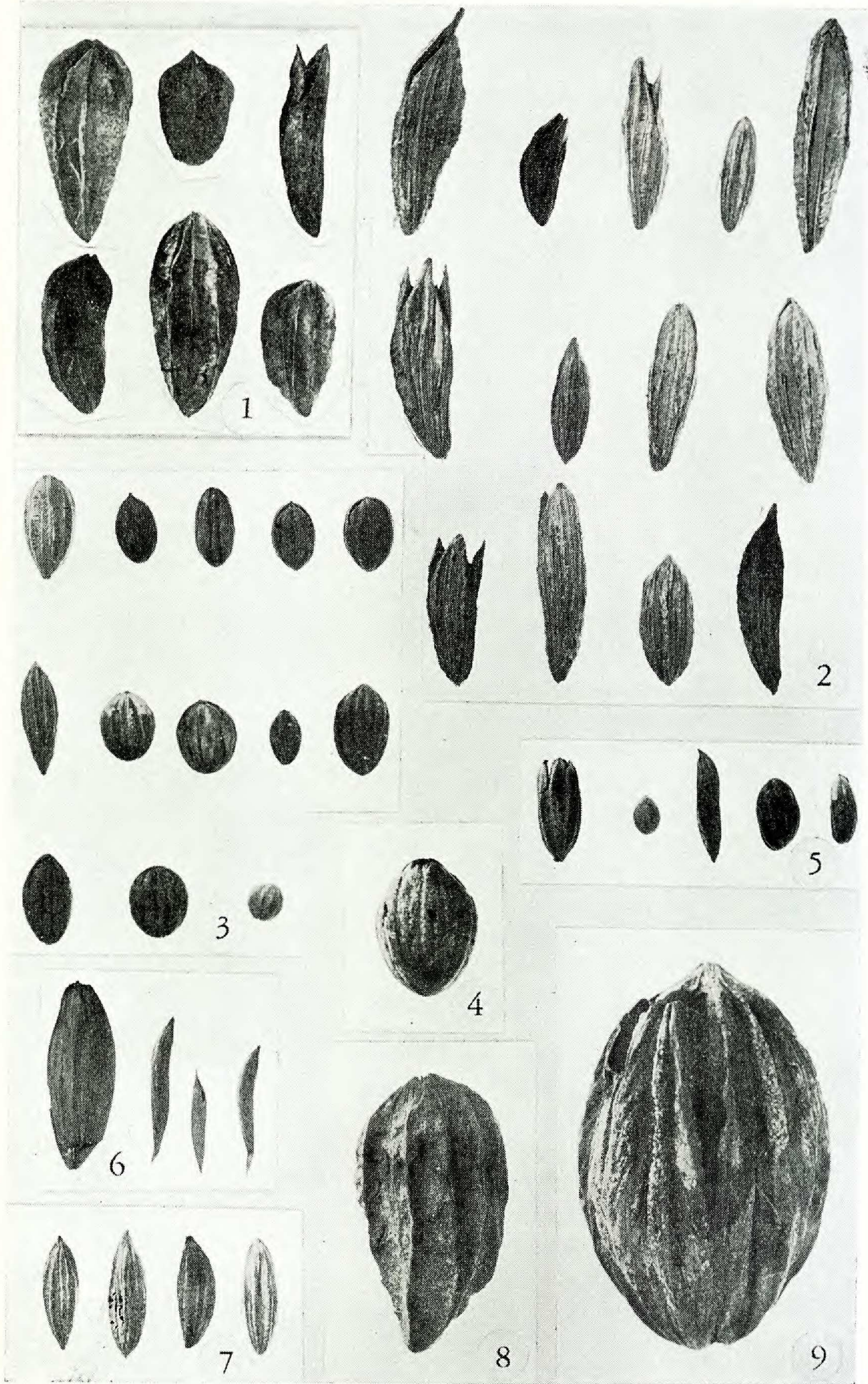
peripheral bundles at junction of carpellary and noncarpellary tissues — note presence of median dorsal bundle and two flanking bundles in lower part of photo. Ovular traces are prominent within the young endocarp tissue. FIG. 16. Transverse section, $\times 30$, of a slightly older ovary (collected June 13th), showing more advanced differentiation of endocarp tissue. The central of the three major tissue zones will be relatively much wider in the mature fruit and will be quite succulent. Dark cells shown in this zone are probably destined to become stone cells. FIG. 17. Part of a transverse section, $\times 30$, of *Davidia* flower — note staminal bundles near periphery of section and discrete carpellary bundles at outer boundary of young endocarp tissue. Dorsals are identifiable by their median position opposite each ovule and flanking bundles by their sunken position. Ventrals lie opposite the septa, are difficult to distinguish from minor carpellary strands in this section. FIG. 18. Transverse section, $\times 7$, dried fruit of *Mastixia arborea* (J. H. Lace 5641, A) — note position of dorsal carpellary bundle in outer part of infold and thickening of endocarp wall in vicinity of ovular traces.

PLATE IV

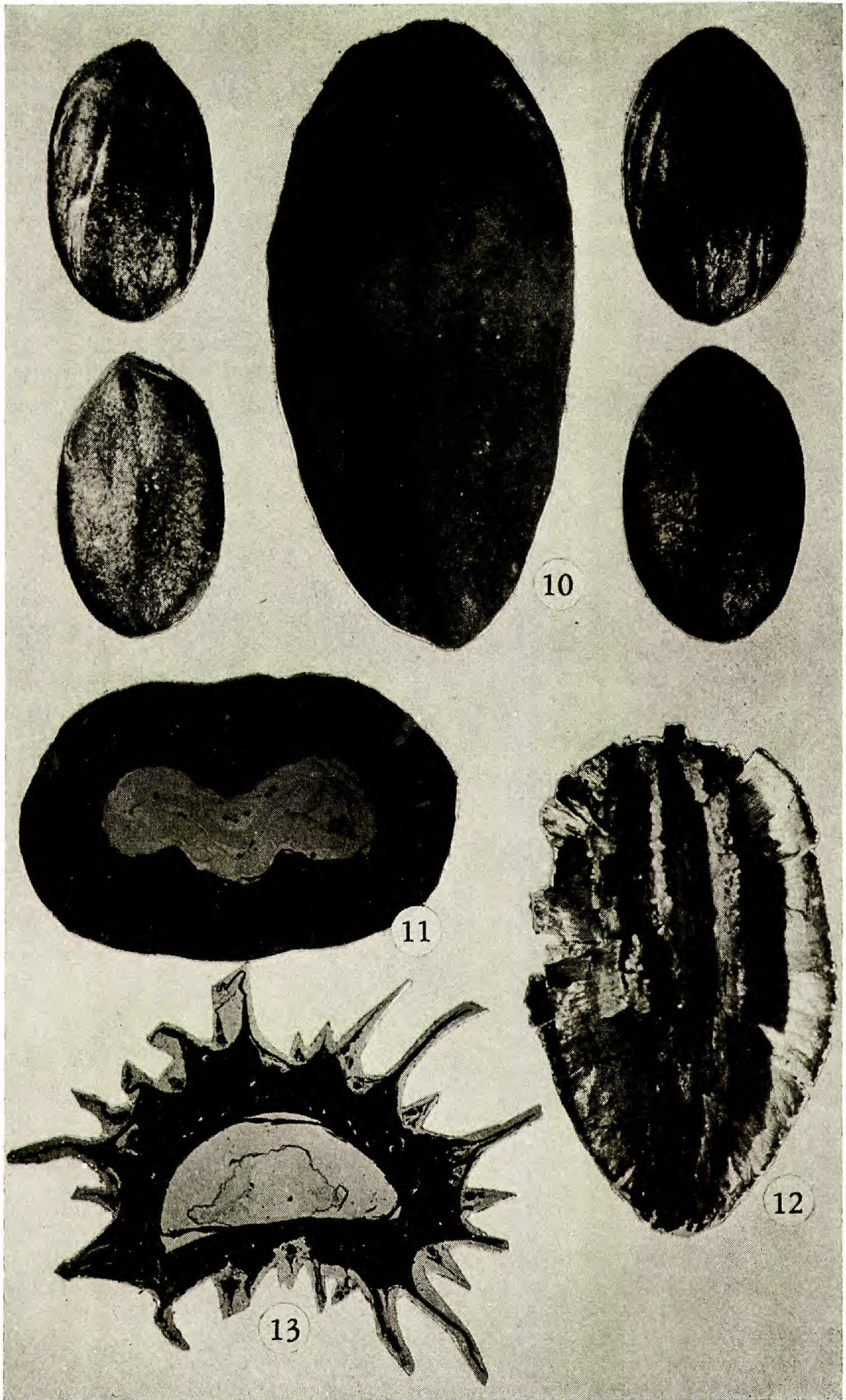
FIG. 19. Transverse section, $\times 5$, of *Davidia* stone, showing two fertile and five abortive locules, germination valves, and numerous ovular traces within the septa. FIG. 20. Transverse section, $\times 200$, of *Nyssa sylvatica* ovary, showing early stage in development of endocarp — note single epidermal layer surrounding locule (above), transversely elongating cells near epidermis and near large peripheral bundle.

PLATE V

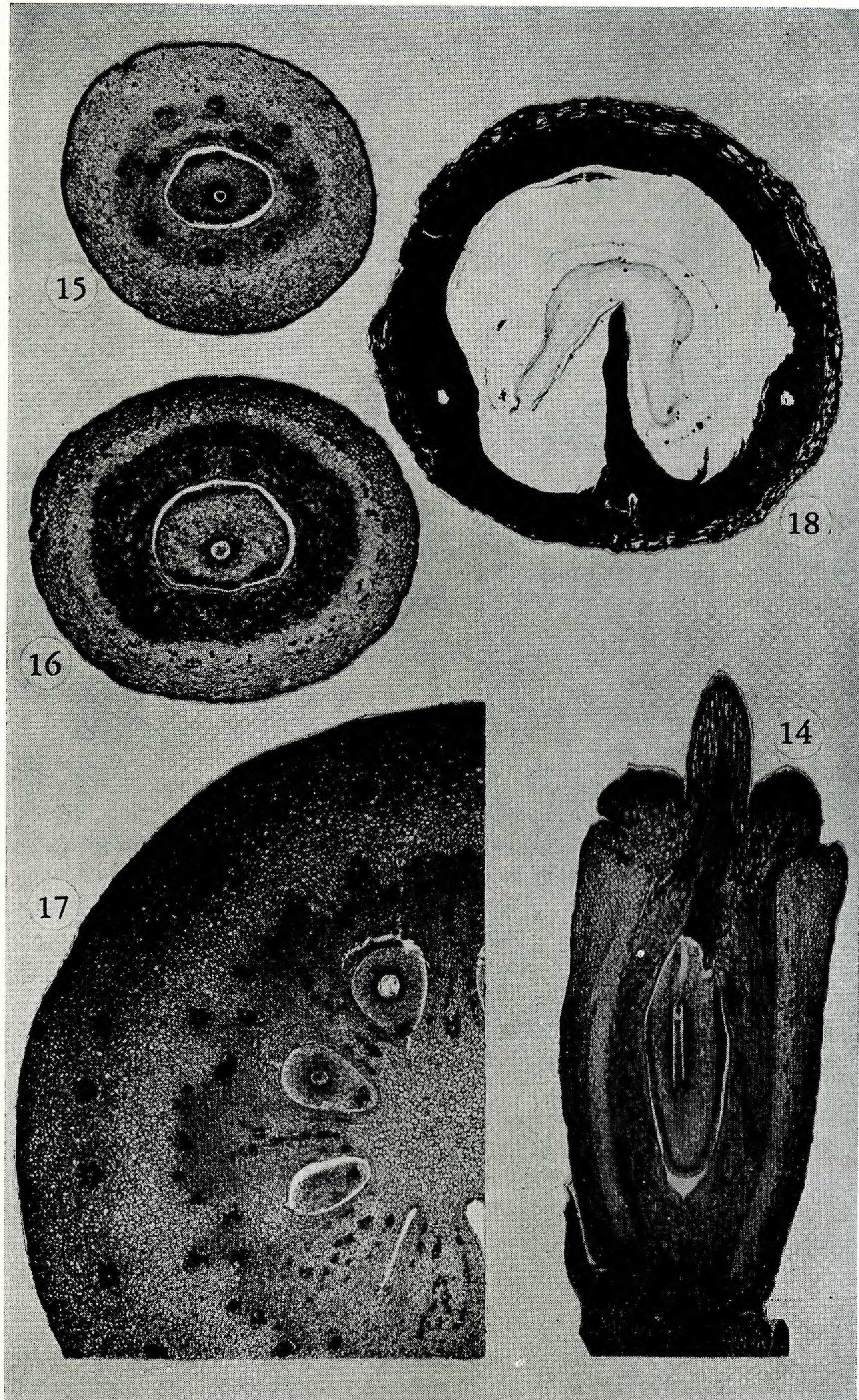
FIG. 21. Dehiscence region, $\times 50$, of *Mastixia* section shown in FIG. 18 — note predominantly longitudinal orientation of fibers; hollow space forms when ovular trace deteriorates; locule is to left. FIG. 22. Ventral region of same section, $\times 50$, showing orientation of elements; part of raphe may be seen in locule (upper left). FIG. 23. Transverse section, $\times 50$, of dorsal portion of *Nyssa javanica* stone, showing orientation of fibers; locule below. FIG. 24. Transverse section, $\times 50$, through ridge in *N. aquatica* stone, showing histological structure and presence of vascular bundle on crest of ridge.



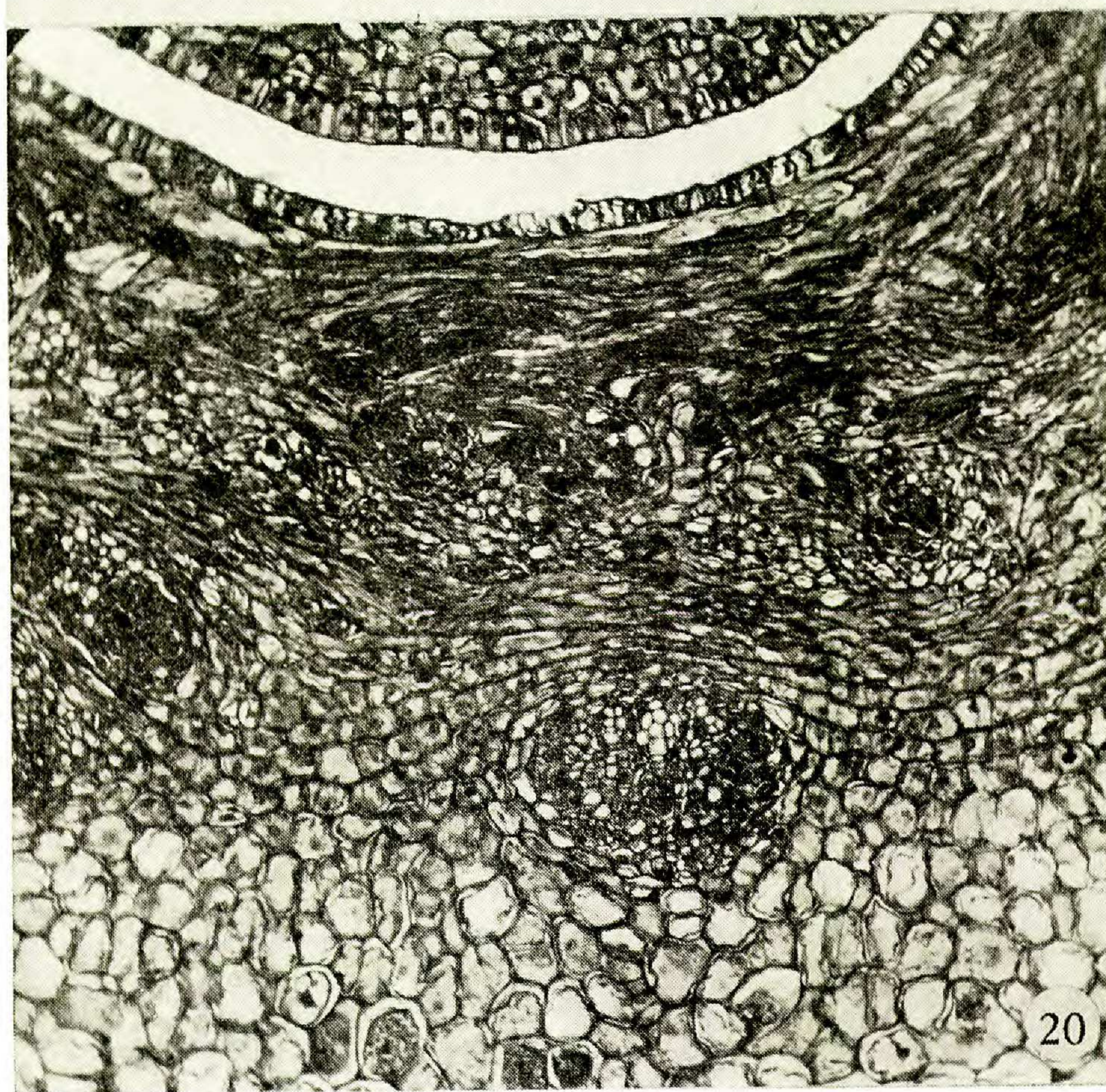
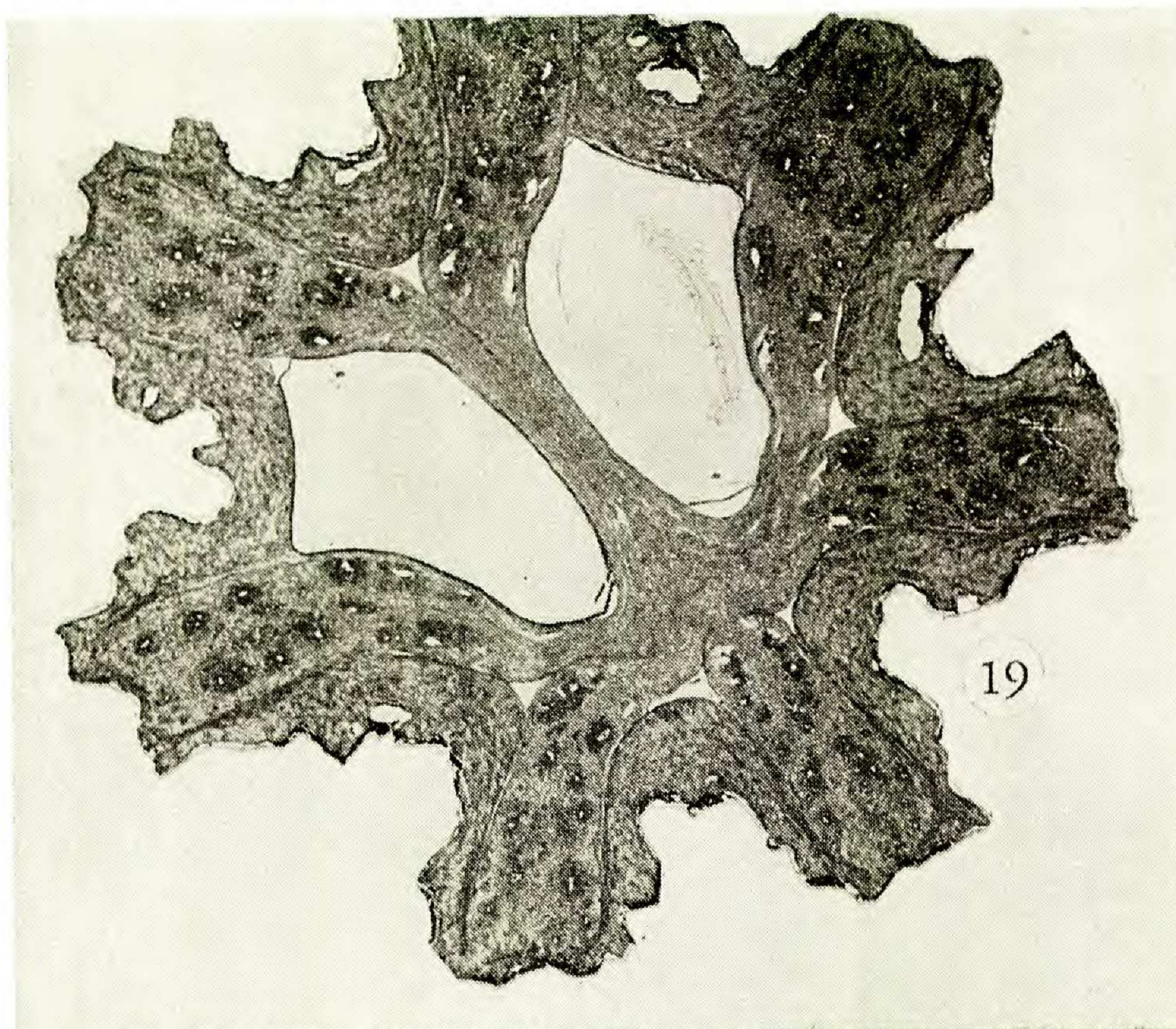
EYDE, STUDIES OF NYSSACEAE, I



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